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by
E. H. FULLING

Advisory Editors

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PROF. R. W. CHANEY, paleobotany
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THE BOTANICAL REVIEW

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DESTRUCTIVE PLANT DISEASES NOT YET ESTABLISHED IN NORTH AMERICA

N. REX HUNT

United States Bureau of Entomology and Plant Quarantine

INTRODUCTION

The welfare of our plants is a matter of vital concern to all of us, for without plants we would soon be without food, clothing and shelter. As befits the importance of the subject, there is a voluminous literature on various phases of plant welfare. From time to time some of the problems involved in the occurrence, development and spread of plant diseases have been discussed. But despite their potential importance, the status of destructive foreign plant diseases, in general, as a part of the plant welfare problem, seems to have received relatively minor attention (22, 72, 96, 106, 107, 125, 128). The continued appearance of serious new diseases in foreign countries, and of new information regarding old foreign diseases; an increased recognition of the seriousness of the problem of foreign virus diseases; the finding of biologically distinct foreign strains of many pathogens; the prospect of increased importations of foreign diseases with newly gathered plant products transported by high-speed aircraft; an increasing knowledge of the possible influence of trace elements, antibiotic substances, bacteriophages, hormones and so forth on the incidence and severity of plant diseases; and the possibility of new methods for eliminating some of the risks inherent in plant importations—these changes, and impending or possible changes in conditions, make it desirable to review the status of destructive foreign diseases with greater frequency.

Destructive plant diseases introduced from abroad are costing us millions of dollars a year for control, millions of man-hours in the production of the hosts whose usefulness they destroy, and incalculable losses in economic and other adjustments and in lost beauty in landscapes and gardens. Other diseases not known to be es-

tablished on the North American mainland appear to be capable of causing great additional destruction. Some of our introduced diseases, such as citrus canker (72) and chestnut blight (63), were unknown until they began destroying plants here. Others, such as white pine blister rust (72) and Dutch elm disease (85), were known to be destructive abroad before they reached us. The powdery scab of potato was so serious elsewhere that its introduction was greatly feared, until it was found to be well established here and usually unimportant. Some of the factors affecting destructiveness will be discussed later. They are sufficiently complicated to make it impossible, on the basis of present knowledge, to predict with certainty what will be the future status here of specific foreign diseases that may be introduced.

Our information regarding even the older destructive foreign diseases, and the pathogens causing them, is entirely inadequate in many essential details to enable us to prepare complete defenses against them effectively and economically. Such data as have been published regarding foreign diseases are to be found in thousands of books and articles, frequently in difficult foreign languages, or in obscure or little-known publications. No attempt is made in this review to list or even to summarize these individual items as such. Instead, a few dozen diseases were selected, and this paper is based primarily on data regarding them. While our knowledge of these diseases is far from complete, the examples selected illustrate the complex factors which must be taken into account in evaluating the status of foreign plant diseases. The pathogens, or causal agents, of the diseases selected include various kinds of fungi, bacteria, viruses and nematodes, a diversity of methods of reproduction, survival and spread, and an equal diversity of ecological conditions favorable to their development. These pathogens have different hosts, including plants used for food, feed, forage, fiber, timber, and ornamental or other purposes. These pathogens may affect their hosts by causing root rots, stem rots, cankers, leaf spots, fruit spots and rots, disfiguring diseases, sterility and wilts, or having other more general effects. Furthermore, the examples selected illustrate the fact that all foreign continents and many islands harbor destructive plant diseases not yet established on this continent.

A disease may be considered destructive if it causes small but widespread losses on a major crop, such as wheat, corn or potatoes,

or if it causes severe losses of useful plants of any kind. Any disease may be considered to be established if the available information indicates that it is here to stay, but not if it is being eradicated, as are citrus canker and potato wart.

EVALUATING DESTRUCTIVENESS OF PLANT DISEASES

There is no standard method of evaluating the destructiveness of plant pathogens. This is readily understandable when the variations in hosts, diseases and circumstances are considered. We speak of destructiveness from the point of view of man, which is not necessarily that of the host. Potted foliage plants might be disfigured and ruined for sale purposes by a leaf spot even though the growth, vigor and reproduction of the host seemed unimpaired. For other plants, grown for fruits or seeds, such leaf spots might be unimportant. Approximately two-thirds of the pathogens listed in this paper affect leaves, and about the same proportion affect stems of their hosts.

In some cases, such as the leaf and stem diseases of grasses[1], lespedeza, sugarcane and hemp, the leaves or stems may be the important crop part of the plant; but in others, such as flag smut of wheat, maize streak and pea rust, the seed is the important crop part, and for beet curly top, the rust of carrot and sweetpotato scab, the fleshy roots or tubers are the crop part of the host.

In tristeza and mal secco of citrus, court-noué of grape, smut of *Brassica* spp., root rot of asparagus and *Vialina* on pyrethrum the roots or lower part of the stem become affected. In three of these plants the crop is fruits; in one it is roots, leaves or seeds, depending on the host species involved; in another it is young stems; and in the last it is flower parts and stems. In potatoes the crop is tubers. Wart and buba disease ruin potato tubers, but the virus diseases and golden nematode may reduce the yield by weakening the plant rather than by destroying the tubers. When a plant is weakened, as well as when the salable part is blemished, the quality or grade as well as the volume of the crop may be reduced. Thus, reduction in yield (including quality) of the crop part of a plant is frequently a secondary effect of the pathogen, and estimates of the reduction are subject to error, but estimated yield reduction seems to be the best measure of the destructiveness of most pathogens.

[1] See section, Examples of Destructive Foreign Diseases.

There are, however, other losses to consider in any discussion of destructiveness of plant pathogens. The beauty of a landscape may be changed or ruined with little change in real-estate values even though the esthetic loss appears to be heavy. If a crop is destroyed early in the season, the ground may be replanted and the net loss greatly reduced. A partial crop may bring such high prices that crop loss is largely or wholly compensated for, insofar as net cash return is concerned.

Many pathogens and pests, as well as adverse growing conditions, may be inextricably combined in causing losses. Loss of ground cover may increase soil erosion, increase flood damage and affect power production with resulting disruption of industry. Crop losses which cause shortages of raw materials for industry, resulting in lost jobs or reduced earnings and consequent lowered standards of living, are losses difficult to evaluate. Crop losses which increase the cost of living of industrial workers are important whether the grower loses money or not. Likewise, crop losses, actual or threatened, which force the grower to work overly long hours to protect his crop, maintain his yield and make ends meet cannot be evaluated readily. In some crops the margin of profit is so small for many growers that an additional relatively small percentage loss might be disastrous.

Despite the impossibility of evaluating either direct or indirect losses accurately, the fact remains that plant diseases, new or old, sometimes cause heavy losses and force economic readjustments which are painful to many people.

FACTORS AFFECTING THE DESTRUCTIVENESS OF PATHOGENS

Some pathogens are more destructive than others, and the destructiveness of a given pathogen varies with conditions. Disease incidence is usually dependent on the interaction of several factors, and the outcome of the interaction is not readily predictable, even where records of the results of more or less similar combinations in the past are available for the same area. It is obvious, therefore, that we are in no position to predict with accuracy what will be the action of each specific destructive foreign disease which may be introduced in the future. However, if suitable data are obtained from foreign areas where those diseases occur, predictions based on such data will be approximately correct much of the time. Some

of the factors that affect the destructiveness of plant pathogens are mentioned in the notes that follow.

Virulence of pathogen and susceptibility of host. The destructiveness of a pathogen depends, first, on its virulence, which may vary in different individuals or strains of the pathogen, and second, on the relative susceptibility or resistance of the host, which varies with species, varieties and individuals, and with age and other conditions. "Resistance" is used here as a general term to include any chemical, physical or other characteristic which hinders infection by, or development of, the pathogen.

Few pathogens, either foreign or domestic, act with the swift destructiveness of common downy mildews, such as *Pseudoperonospora cubensis* (Berk. and Curt.) Rostew. on cucurbits, or of potato late blight (*Phytophthora infestans* (Mont.) D By.), which may cause the sudden collapse of their hosts over considerable areas of a planting. Many pathogens, however, are destructive enough to eliminate possible profits by killing their hosts prematurely or by destroying or limiting their usefulness in some way. Orange trees affected by tristeza (155) may die in a few months after they become infected. In lemon trees infected with mal secco (110) the fungus grows upward at the rate of about two feet a month, soon killing the tree if infection takes place in the roots or lower part of the tree, but growth downward from infected twigs is very slow and death from such infections does not result so quickly. In carnations *Verticillium cinerescens*[2] (160) was found to have a mean rate of growth of approximately 0.6 cm. per day during June and July, and 0.4 cm. during September and October. The virus causing pupation disease of oats (139) is able to spread through host tissues at the rate of 7 cm. per hour, fast enough to invade an entire plant in a quarter of a day or less, but the host is stunted and made abortive, rather than killed as soon as invasion of the tissue is completed. The rate of movement of the maize streak virus (132) varies, but is said at times to exceed 20 cm. per hour down infected leaves.

Cronartium flaccidum rust (15) of hard pines stunts and ruins affected hosts but does not necessarily kill affected tissue; in fact, the affected tissue is rather fully invaded for some time before the fungus is ready to produce spores. Maize streak (133) is ruinous

[2] Authors for binomials listed in the section Examples of Destructive Foreign Diseases are not given elsewhere.

on infected seedlings but does little damage to plants not infected until nearly mature.

Variations in virulence of pathogens have been studied in rusts and smuts, especially, and numerous fairly constant strains, races or biotypes have been differentiated. New strains of various pathogens frequently arise through interbreeding of closely related forms or through mutation. These strains vary greatly in their virulence on a given host. Closely related host varieties also vary greatly in their susceptibility to infection and in the degree of injury induced by infection with a given strain of a pathogen. One would expect a pathogen or strain which is extremely virulent on a host to destroy it, as the chestnut blight (63) seems to be eliminating American chestnuts, but that does not necessarily follow. If a few individuals with some resistance are able to reproduce, and such of their offspring as are resistant continue to reproduce for a number of generations, the time may come when susceptible hosts no longer appear, and the pathogen seems to be nonvirulent. If this pathogen is taken to a new locality, or if a new supply of susceptible individuals is brought in, it may demonstrate its virulence again. Virulence of a pathogen to a given host is sometimes modified by its growth for a time in another host. Some strains of *Glomerella cingulata* (Ston.) Spauld. and Schrenk and of *Ditylenchus dipsaci* (Kuhn) Filip. will readily attack a wide variety of hosts. Other strains, long confined to a single host or a small group of related hosts, seldom invade other species. Peanut rosette (122) has been transmitted to *Centrosema plumieri,* but attempts to transfer it back to peanut have failed.

Some of the leafhoppers which transmit rice dwarf (46) must feed on diseased hosts much longer than others in order to be infective, and some do not become infective at all regardless of the time of feeding. The feeding periods required to make infective the individual vectors of the pupation disease of oats (139) are extremely variable also, the minimum being six hours, and never do more than 37% of the insects present become infective, even though all the oat plants are diseased. Vectors of maize streak (134) vary greatly in their ability to transmit the disease, and some races or groups of the insect species involved are not vectors, although some are able to act as vectors if the virus is artificially injected into them. The causes of variations in the ability of individuals to transmit virus diseases have not yet been determined.

Host plants transferred to new areas may be severely attacked by diseases of related plants in the new home. This happened to corn sent to the Orient, where the downy mildew of sugarcane and other related plants attacked it. However, if corn varieties developed in the Orient for resistance to downy mildews were brought back to this country, they might be found to have lost resistance to some of the destructive diseases here. Combining resistance to disease with quality and yield in new plant varieties is a major problem of breeders, and the frequency with which pathogens appear in the form of new races which are virulent on host varieties resistant to the old races makes it necessary to continue to develop new varieties, even if no new species of pathogens appear. New races of potato wart (18) in Germany are destructive on nearly all varieties developed for resistance or immunity to wart. New races of flax rust (148) in Argentina are destructive on new varieties bred for resistance to the rust forms in our flax areas. Races of flag smut in China (168) affect different groups of wheat varieties and might be severe on varieties resistant to any flag smut strain we have in this country. A large proportion of our important crop plants were introduced many years ago. Many diseases were introduced with these plants, but in the intervening years new races of the pathogens may have developed in the countries of origin, and selection and breeding may have led to radical changes in both host and pathogen in this country. Hence our choice varieties may succumb to common diseases if they are taken abroad, or if present-day strains of the pathogens are imported from abroad.

Absence of a pathogen or a race of a pathogen during one season is no assurance that it will be absent the next season. Asparagus root rot (156) reappeared after apparent absence for nearly 50 years and destroyed up to 80% of asparagus plantings in the type locality. The predominant strains of the much studied black stem rust of wheat have varied from year to year in unpredictable fashion. The rose wilt virus (54) may be destructive for several years and then appear sporadically for a year or two.

It is known that the vitamin content of plants used for human food varies with individual plants, with varieties, with species, with the soils in which the plants are grown and with conditions of growth. Similar variations of chemical compounds occurring in infinitesimally small amounts may account for some of the variations in the

susceptibility of host plants, and in the virulence of pathogens growing on them. That is, lack of optimum amounts of vitamins or of trace elements or compounds in the plants may weaken their resistance to some diseases. Again, inability of the pathogen to obtain optimum amounts of some vitamins or trace elements from the host may weaken its parasitism (56, 117). It is known that bacteriophages (69), or virus diseases of pathogenic bacteria, occur. However, our knowledge of the effects of trace elements, of bacteriophages, of antibiotic substances produced by various hosts or organisms and lethal or inhibitory to some pathogens, of vitamins that may be needed by hosts and by pathogens, and of hormones affecting them, is too fragmentary to enable us to evaluate their rôles in regulating or determining the virulence, or apparent virulence, of destructive foreign pathogens or the susceptibility of hosts to such pathogens.

Reproductive capacity of pathogen. The reproductive capacity of the pathogen is another factor in determining its destructiveness. A pathogen which killed every host infected but which seldom produced a new infection might be unimportant and soon die out. Pathogens causing rusts, downy mildews and brown rots usually produce enormous numbers of asexual spores, often in several generations, during a single growing season. Smut fungi usually produce great numbers of spores, sometimes millions in a single mass, and each of these in turn may produce a number of sporidia—150 in a whorl in Karnal smut of wheat (99). Enormous numbers of bacteria are produced in infected hosts, as, for example in gumming disease of sugarcane (39, 122) and *Aplanobacter rathayi* (39, 122) on *Dactylis*. Such organisms, if distributed under favorable conditions, may cause so many new infections close together that infected leaves or stems will be killed very quickly. Viruses may increase very rapidly (8, 132, 139), destroying the usefulness of affected host plants, which at the same time become potential sources of infection. Multiplication of the virus in insect vectors is claimed in the case of rice dwarf (45), but there is a difference of opinion regarding the conclusiveness of the evidence (8). The troublesome nematodes may produce several generations a year and have numerous offspring each time. The black currant nematode reproduces throughout the year but most rapidly in the spring (97, 143). The nematode causing ufra disease of rice apparently does not

multiply during the winter and spring, but even so, masses of new nematodes are produced on the host for three or more generations each year.

The amount of multiplication of a pathogen required to cause an epiphytotic is not measured by number or volume alone. Theoretically, a thousand spores may be able to infect and kill a thousand plants, but in practice the number of infected individuals per thousand host plants may be a hundred or fewer even, though billions of spores per plant are available. The spores must reach a large proportion of the hosts alive and under conditions favorable for infection, or there is no heavy infection, and the effective combination of all necessary factors just doesn't occur for most spores. However, the number of spores a fungus must produce to be destructive obviously depends on the effectiveness of its distribution and infection system. Air-borne spores, such as downy mildew or brown rot conidia and rust spores, which are scattered over large areas where infection is seldom possible, must be produced in vast numbers to insure even a moderate incidence of disease. Yet the perfect stage of downy mildews, produced in much smaller numbers but carried with the seed or left in the soil where the host will be planted again, may show a relatively high incidence of disease per billion spores produced.

Ability of pathogen to spread or to reach its host (22, 49, 62). Ability of a pathogen to spread, or to be spread, is a major factor in its destructiveness. Production of masses of spores or other forms of inoculum is not enough. The inoculum must reach numerous hosts by the aid of air currents, rain, insects or other animals, or on tools or farm machinery; or, in the case of pathogens carried over in the soil, hosts must be grown in the same soil again in order to cause epiphytotics. Spores of rusts (89), smuts (72, 99, 149), downy mildews (72, 159), and many others, as well as bacterial pathogens such as the one causing ash canker, are usually spread by air currents or splashing rain. The black currant nematode travels in water or is blown about when in a dry state (143). Dutch elm disease would probably be of relatively minor importance without the insect carriers of the pathogen. Many virus diseases, such as pupation disease of oats, rice dwarf, wallaby ear and maize streak of corn, are dependent almost entirely on insect vectors or carriers for their local spread. The incidence of pupation disease

may be greatly reduced by providing barriers two meters high between oat fields and the fence rows, which are covered with grass and weeds on which the larvae of the vectors overwinter (138). The potato wart fungus is spread locally by water, and on tools and the feet of man or other animals. Many disease organisms are spread from place to place on a farm or to outside areas on seeds, plants or plant parts transported for food, feed or manufacturing purposes.

The spread of pathogens, both local and long-distance, is affected by continuity and size of plantings of the host. Stem rust of wheat starts in Mexico, and wheat plantings in the Mississippi Valley are so large and so nearly continuous that air currents sweeping the spores north cause new infections which supply additional spore crops and enable the rust to reach Canada by relays before the season is over. One-crop areas and pure stands of forest trees make it possible for pathogens, once started, to produce epiphytotics, even though their spore production and their individual distance of spread are rather limited. Of course, if wild hosts abound, pathogens may spread on them between scattered plantings of cultivated hosts. White pines may be well scattered and still succumb to white pine blister rust if aeciospores or urediospores are spread by air currents from distant points to ribes plants nearby. The chestnut-blight pathogen and other fungi produce such enormous numbers of wind-borne spores that isolated hosts may receive some of them and become infected. Insect carriers, birds, *etc.,* may aid pathogens in overcoming the theoretical advantage of isolation.

Sometimes there are special problems in the dissemination of pathogens. For example, the downy mildew (*Sclerospora sacchari*) affecting sugarcane and corn in Australia produces large numbers of short-lived conidia on corn but not on sugarcane; therefore the presence of corn plantings is necessary if the disease is to spread rapidly during the growing season. Gumming disease of sugarcane produces quantities of bacterial slime, but there seems to be little spread from diseased to healthy plants in the field, except where the soil is wet. Spread results largely from the use of infected canes for propagation purposes.

Court-noué of grape is spread by propagation from diseased plants. The same is true of potato viruses, tristeza disease of citrus, downy mildew of sugarcane, black currant nematode, and others.

While some pathogens, such as *Neovossia indica* of wheat, *Botrytis anthophila* of clover, *Pleospora calvescens* of poppy and soybean *Fusarium* disease, are carried in seed tissues, about a dozen others of those listed are carried as spores or otherwise on seeds or accompanying fragments of host tissue. Since such organisms are likely to be scattered through new plantings, only short distances from the initially diseased plants need to be bridged to bring about infection of all plants. Dodder plants have been found to transmit a virus disease from one host to another (11). Although it is not yet accepted as fact, there is evidence that crown gall is a virus disease of which *Bacterium tumefaciens* E. F. Sm. and Towns. is the vector instead of the causal agent itself (17, 56, 162, 163). If virus diseases are carried by bacteria and fungi to new hosts, some of the unimportant pathogens may take on a new importance. Virus diseases present a particularly difficult problem in prevention of disease spread, because there is no practicable method for detecting their presence in much of the plant material that is moved, even if the pathogen is present in abundance. Plants of little economic importance may appear to be disease-free throughout their lives and yet carry viruses destructive to important crop plants. Such masked carriers might be widely distributed and cause heavy losses without being suspected.

The probability of entry, establishment and spread of dangerous foreign diseases seems likely to be further augmented by increased use of aircraft in transporting freshly gathered fruits, vegetables and plants from all parts of the world. Incipient infections, viruses and adhering spores would be impossible to detect, by present inspection methods, on such materials at the time of arrival. By the proposed air routes, materials could be delivered to hundreds of scattered markets not far removed from our growing areas, instead of to a few big cities, mainly on the sea coast, where there is relatively little chance for a pathogen to survive. Mass movements, as a result of the war, have doubtless spread diseases into new areas. It seems certain that man's actions will combine to increase the likelihood of the introduction and spread of destructive foreign diseases, unless man devises and puts into effect improved counter measures.

Ability of pathogen to survive. A pathogen must be able to survive under unfavorable conditions if it is to be recurrently destructive. In mild climates, with hosts available at all times, a pathogen

such as that of a rust or a downy mildew or a brown rot may persist indefinitely merely by producing short-lived summer spores. But over much of the world there is a cold season, or a dry season, or a host-free period, which must be bridged if a pathogen is to persist.

Many fungi, such as those causing potato wart, downy mildews and rusts, produce thick-walled spores able to retain viability through periods of cold or drought, or even for several years. Such resting spores of potato wart and downy mildew fungi may spend the off-season in the soil, sometimes remaining there for several years before the right combination of factors induces germination, or they may remain above ground in debris on the soil, or in storage places, and germinate later if given an opportunity. *Choanephoroidea* on squashes mummifies infected flowers and fruits, and these mummies doubtless serve as sources of infection the following season. Other fungi, such as the brown rot organisms, produce sclerotia that withstand unfavorable conditions. Still other fungi, such as the apple scab pathogen, may persist as saprophytes on dead leaves and in spring produce a perfect stage which starts new infections.

Many viruses and some of the rusts, smuts and downy mildews are systemic in perennial hosts; so if the host survives, the pathogen is likely to survive also. Some pathogens survive on or in hosts other than the one of particular economic value. The fungus causing shab disease of lavender, for example, can live through the winter as a saprophyte on dead goosefoot plants as well as on dead parts of lavender. *Cronartium flaccidum* rust of hard pines has numerous telial hosts, some of which are not of economic value. Many pathogens overwinter in seeds, among them being *Aplanobacter rathayi* of cocksfoot grass, *Botrytis anthophila* of clover, *Colletotrichum indicum* of cotton, and perhaps the mosaic of subterranean clover. Among the viruses that survive from season to season in insect vectors are those of pupation disease of oats (139) and of dwarf disease of rice (45). Some pathogens, such as those of common potato scab (*Actinomyces scabies* (Thaxt.) Güssow) and cotton root rot (*Phymatotricum omnivorum* (Shear) Dugg.), may live indefinitely as saprophytes in the soil and then attack hosts when they become available. Other pathogens, such as those of chestnut blight, white pine blister rust and Dutch elm disease, may remain viable and sporulate on host material after the host has been cut down.

It has been known for a number of years that some fungi are antagonistic to other fungi or to bacteria (47, 86, 111, 150, 151, 152). The most publicized cases of such antagonism are those involving penicillin, but there are numerous others. While considerable work is being done in this field, we have no specific data to indicate that any fungi or bacteria antagonistic to any of the destructive foreign pathogens discussed in this paper would aid in preventing their establishment here, but such a condition is quite possible. Even so versatile a creature as man failed in many of his early attempts to establish colonies in the New World. Introduced colonies of plant pathogens sometimes may find it just as difficult to contend with antagonistic native organisms and new conditions as did the early settlers with Indians and unfamiliar conditions.

Ecological conditions as related to host and pathogen (90, 164). Ecological conditions often determine the destructiveness of a pathogen. In general, hosts are grown where ecological conditions are favorable for their growth, and only such pathogens as are able to thrive under the same conditions will be destructive to the hosts. However, it is well known that some pathogens are especially destructive during a wet year, or following periods of rain or following early rains and mild temperatures or some more or less specific combination of ecological factors. Regulation of planting dates to avoid having seedlings in a susceptible stage at the time ecological conditions are likely to be favorable for infection is practiced in controlling flag smut of wheat, for example, and may be used for pupation disease of oats (138) and flax rust (148). Many of the virus diseases are dependent on insects for spread. Unless conditions are such that fairly large numbers of the insects may be present and may become infective at a time when the hosts are susceptible to destructive attack, no epiphytotic is likely to develop. Losses from wallaby ear of corn may be greatly reduced or nearly eliminated by planting corn early enough so it will be nearly mature before the vectors become prevalent after midsummer. The beet leafhopper (*Eutettix tenellus* (Baker)), which is the vector of curly top in our western States, is a dry-atmosphere insect by preference. Not only is this insect confined to more or less arid regions, in its natural distribution, but it does not thrive in the beet fields if the beets are large enough to make considerable shade and attendant increased humidity before its winter hosts dry up and force migra-

tion to the beet fields. However, the vector has been transported to other areas and may be sufficiently adaptable to become permanently important under different conditions. Spread and development of peanut rosette, transmitted by *Aphis medicaginis* Koch (*A. leguminosae* Theob.), is increased by dry weather, and thick sowing gives partial control. Maize streak was unimportant in South Africa in 1935–1936, when spring rains were light and very late; but infection was nearly 100% the next year when spring rains were early and abundant. The higher humidity increased rather than decreased the transmission of maize streak by its vector.

The pycnidia of the mal secco fungus on lemon are blown about by the wind, and release spores when sufficient moisture is present. In laboratory experiments it was necessary to maintain abundant moisture, either free water or 100% humidity, for 40 hours or more at 15° to 16° C. in order to obtain spore release, germination and infection (109). The banana leaf spot (*Cercospora musae* Zimm.) (?), which has created such havoc in the Caribbean banana-growing areas in recent years, seems to require three or four successive nights of high humidity and moderate temperature (80° F. or lower) in order to infect banana leaves. The foreign *Sclerospora* downy mildews of corn (72, 157, 158, 159) would be unlikely to produce epiphytotics in this country except in areas with warm humid nights, but those are the good corn areas. Some foliage diseases are destructive where the hosts are crowded, with consequent increase in humidity, but are not serious otherwise. Damage from the *Pleospora* which causes drying out of poppy leaves is worse in hot than in cool seasons (112). The nematode causing ufra disease of rice and the one destroying black currant buds are relatively unimportant in the absence of moisture films on the stems (143). If hosts requiring considerable water are grown under irrigation in areas where the air is normally dry, pathogens depending on a humid atmosphere for destructive spread may be found to be unimportant. The relatively dry atmosphere in California's irrigated citrus areas is thought to account for the fact that citrus canker and black spot have never become established there, even temporarily, and that melanose is unimportant. The highest incidence of *Colletotrichum indicum* on cotton is in soils with 30% to 50% of moisture, the optimum for seed germination being 50% (144). Many rusts and other fungi are found in arid

regions, but they require the presence of rain, dew or other moisture to start new infections. The potato wart fungus seems to require a short growing season and low soil temperatures to persist; so it should not be feared in the southern States. On the other hand, flag smut of wheat does not appear to be able to exist in cold northern wheat-growing areas.

Some pathogens, such as that of club root of cabbage, do not thrive in alkaline soil, while others, such as that of potato scab, are less destructive in acid soil.

In addition to the more or less direct effects of heat, light, moisture and soil acidity on the pathogen, these factors affect the host and its susceptibility to destructive attack. The presence of moisture in the air may keep stomata open for entry of germ tubes of spores of black stem rust of wheat, banana leaf spot, and numerous others.

A crop barely able to obtain the minimum amount of water for healthy growth may be destroyed by a pathogen that reduces the effective root system by rotting a few roots or root tips, that invades the vascular system and obstructs the flow of sap, or that increases water losses by inducing cracking of tissues, preventing the closing of stomata, or otherwise. Even where soil water is abundant, severe reduction, in one or more of these ways, of the amount used by the host may be destructive. Roots may become soft and easily invaded by water-loving pathogens in the soil if the soil becomes waterlogged. Gumming disease of sugarcane is particularly severe on low, wet or poorly drained soil.

Sudden drying of wet soil may cause it to crack, and thus injure roots and give parasites an entrance point, or may cause the plant to wilt because of insufficient root hairs to take in water, so that pathogens may invade and grow rapidly through the weakened shoots. Shoots injured by cold are favored points of entry for the pathogen causing mal secco of lemon.

Difficulty of control of pathogen. The difficulty of controlling a pathogen will in many cases determine the extent of the damage inflicted by it. If treatments, sanitation, crop rotations, certified seed systems or the use of resistant varieties required to control diseases already here would be sure to control a specific disease not yet established, there would seem to be little to fear from it. However, if, in spite of the control obtained, an additional 5% loss

should be caused, the margin of profit might be eliminated and serious financial losses result.

As indicated in the discussion of the effect of ecological conditions, it is sometimes possible to obtain some degree of control by changing planting dates. But if planting dates of a crop are now set to avoid local diseases, pests, adverse weather or soil-moisture conditions, the importance of a new disease might depend on whether or not new and otherwise less desirable planting dates would be required to control it.

When an alternate host is required to enable a destructive disease to persist, control might depend on the possibility of eliminating one host or set of hosts. White pine blister rust is controlled by eliminating currant and gooseberry plants, but the foreign rust (*Cronartium flaccidum*) of hard pines has so many diverse hosts that elimination of all of them would probably be impracticable. Pathogens which, like this rust of hard pines, are able to infect a number of different hosts readily, may be sufficiently adaptable to be able to spread to additional hosts and to handicap efforts to breed or select resistant varieties. Virus diseases seem to be particularly likely to affect diverse hosts.

Virus diseases requiring insect or other vectors or carriers that are not present in this country, in order to spread appreciably, would not be destructive here unless the vectors were introduced also and were able to survive and multiply under our conditions, or unless native insects were able to transmit the viruses before the infected hosts succumbed. The vector *Eutettix tenellus* of the sugar-beet curly top virus in this country has been found to be incapable of transmitting the somewhat similar virus disease that occurs in Argentina. The tristeza "virus(?)" of sour orange stocks can be brought under control in an affected sweet orange tree by top-working it with lemon or sour orange, the leaves of which apparently produce some substance which inhibits any evident action by the virus.

High yields of rubber are expected from *Hevea* trees produced from high-yielding strains susceptible to the destructive leaf blight *Dothidella ulei* P. Henn., but completely top-worked so that the leaves of mature trees will be those of another form which is resistant to this disease (78). Promising results have been obtained with a substance (disodium ethylene bisdithiocarbamate) that is

absorbed by plants and makes them lethal to certain pathogens and insects (1, 65, 126). Perhaps further studies on antibiotic substances, fungicides, bacteriophages, ultra-short wave lengths, trace elements, hormones, vitamins and so forth will make elimination or control of now dreaded foreign pathogens easy and inexpensive, and thus reduce their destructiveness to the vanishing point, but no such happy state of affairs can be expected in the immediate future.

POTENTIAL SOURCES OF DESTRUCTIVE FOREIGN DISEASES (19, 128)

Records of diseases found on plant materials coming to our ports (147) show that Italy and Japan have many plant diseases that are not yet established in this country. Italian occupation of African areas for several years and Japanese occupation of numerous islands as well as mainland areas may well have resulted in the introduction and establishment of new diseases in both countries. In Russia the rapid development of agriculture, with the introduction of new plants which are subject to destructive infection by the diseases of native plants, and the employment of a greatly increased number of pathologists to study these plant diseases have led to numerous reports of new diseases occurring there. Acceleration of agricultural development in South America, with increased scientific activity, should be expected to bring to light numerous unreported diseases on that continent.

China with its ancient civilization undoubtedly has accumulated numbers of diseases that, like citrus canker and chestnut blight, would be destructive in this country, even though the cultivated varieties grown in China have been developed through centuries of selection to a high state of resistance. Europe, Africa, Australia and numerous islands continue to report new and destructive plant diseases with disturbing frequency.

EXAMPLES OF DESTRUCTIVE FOREIGN DISEASES

The following examples of destructive foreign diseases of plants show several affecting each general group of hosts, although some of the hosts belong in two or more groups, and some of the pathogens affect hosts in more than one group.

Diseases of plants used for food and feed. Karnal bunt (*Neovossia indica* Mitra) (99) causes up to 20% damage to wheat in the

hot lowlands of India. Cool damp weather favors infection. Both spores and sporidia are wind-blown. Wheat flag smut (*Urocystis tritici* Koern.) (44, 71, 72, 101, 118, 149, 168) occurs in Europe, Asia, Africa and Australia, but not in areas having extremely severe winters. Foreign strains in South Africa cause crop losses up to 90% of susceptible varieties. *U. agropyri* (Preuss) Schroet., a smut of numerous grasses in this country and capable of infecting wheat to a limited extent, is said to be the same species as *U. tritici* (44). Whether merely a series of specialized races of *U. agropyri* or races of a distinct species, some of the foreign races of flag smut seem to be capable of being destructive on wheat in this country, should they become established here.

The pupation disease (96, 138, 139), due to a virus, *Fractilinea avenae* McK., carried by the insect *Delphax striatella* Fallen, is thought to have originated in wild grasses, but is widespread on oats and occurs on other cereals and grasses in Russia. Infections of oats run as high as 100%, with almost total loss of grain production.

The ufra disease (*Ditylenchus angustus* (Butl.) Filip.) (21, 43, 52) has caused heavy losses in rice production in India and is reported to occur in Malaya. Rice dwarf (*Marmor oryzae* Holmes) (45, 46, 70, 76, 79) has caused severe food shortages in Japan. The virus is believed to multiply in a vector (*Nephotettix apicalis* Motch. var. *cincticeps* Uhl.) and is carried in or with the eggs for several generations.

In parts of Queensland, Australia, late-planted corn is subject to wallaby ear (116), a virus disease caused by *Galla zeae* McK., carried by *Cicadula bimaculata* Evans and perhaps by other jassids. Infected plants are dwarfed and yields reduced seriously. Maize streak virus (*Fractilinea maidis* (Holmes) McK.) (70, 114, 132, 133, 134, 135) limits production of corn in parts of Africa. Sugarcane and other grasses are less severely affected. A leafhopper, *Cicadulina mbila* (Naude), is the principal vector. Heavy early spring rains are said to increase infections and make losses very serious.

Gumming disease, *Bacterium vasculorum* (Cobb) R. G. Smith (10, 39, 122, 129), prevents growth of susceptible varieties of sugarcane in Australia, South America, East and West Indies, Mauritius and elsewhere, and also infects corn and resistant vari-

eties of sugarcane. Downy mildews (*Sclerospora* spp.) (9, 10, 72, 80, 92, 129, 130, 157, 158, 159) destructive to corn, sugarcane, sorghum and related grasses, occur in Asia, Africa, Australia and Pacific islands. Not one of the five foreign species infecting corn is known to produce resting spores (oospores) on that host. *S. sacchari* T. Miyake in Australia depends on the enormous numbers of conidia produced on corn for destructive spread on sugarcane during the growing season, as relatively fewer conidia are produced on cane. *S. sorghi* (Kulk.) Weston, in India and Africa, produces few conidia and spreads to corn and sorghum largely through distribution of oospores produced in abundance on sorghum. These downy mildews usually require warm humid nights, as are likely to prevail in good corn and sugarcane areas, in order to produce epiphytotics. Under such conditions they may cause losses of up to 100%. The difficulty of germinating oospores artificially has handicapped study of those fungi.

Another sugar plant, the sugar beet, is subject to a virus disease in Argentina (40) that produces symptoms similar to those of curly top, transmitted by *Eutettix tenellus* in the United States. In all tests *E. tenellus* has failed to transmit the Argentine virus. The vector of the virus in Argentina is *Agalliana ensigera* Oman.

The tristeza disease (12, 155), fatal to most varieties of citrus trees grown on sour orange stocks, is destructive in South Africa, Java, Argentina and Brazil. Apparently the leaves of sour orange and lemon produce a substance which inhibits deleterious action by the causative agent, presumably a virus. Black spot (*Phoma citricarpa* McAlp.) (5, 42) of citrus in Australia and the Orient has recently become established in South Africa and Brazil. Where it has been long established losses may be serious, for the fungus causes the fruit to fall and disfigures harvested fruit, often while enroute to market. The mal secco disease (*Deuterophoma tracheiphila* Petri) (42, 50, 109, 110) has killed almost all lemon trees in some areas, and apparently it will eliminate lemons as a commercial crop in the Mediterranean region unless efforts to replace present plantings with resistant forms are successful. Other citrus species are affected less severely. The fungus grows upward through conducting vessels very rapidly; death results in a few months following root infections, but more slowly following twig infections.

A severe and widespread disease of the branches, leaves and fruits of apple in Korea is caused by *Physalospora piricola* Nose (103, 102), which also causes the destructive ring disease of pear fruits.

The brown rots of stone and pome fruits caused by fungi belonging to the genera *Sclerotinia* and *Monilinia* are already well represented here, but additional forms capable of increasing both destruction and the difficulty of control occur elsewhere. Among these additional forms are *M. fructigena* (Pers.) Honey (166), which is serious on both stone and pome fruits in Europe, Japan and Manchuria, and has been reported from South Africa; and *M. laxa* (Aderh. and Ruhl.) Honey f. *mali* (Worm.) Honey (119, 166, 167), which causes blossom wilt and die-back of apple shoots in Europe and Japan. Conspicuous witches'-brooms with stunted leaves are caused by *Taphrina armeniaca* Georgescu and Badea (51) on apricots in Rumania. This disease appears capable of being very destructive.

The black currant eelworm (*Aphelenchoides ribes* (Taylor) Goodey) (43, 52, 97, 127, 143) destroys buds of black currants in England and New Zealand. A film of water on the stems is necessary to enable the nematodes to reach the buds. *A. ribes* has been called a synonym of *A. fragariae,* based on material in leaves and buds of *Grossularia reclinata* from Albion, Calif. If so, it seems to be a different physiological strain.

Court-noué (16) is a destructive virus disease producing such variable symptoms on grape vines that its exact status and distribution in Europe is confused. *Phylloxera vitifoliae* (Fitch) is said to be a vector, but the disease spreads from one root system to another without aid from *Phylloxera.* Plants of American grapes are very susceptible.

Potato wart (*Synchytrium endobioticum* (Schilb.) Perc.) (18, 61, 72) is destructive in areas having cool soil and a short growing season. It occurs in North and South America, Europe, Asia and Africa. Recently two new strains appeared in Germany and were found to be destructive on nearly all resistant varieties developed through years of extensive breeding work. The small amount of potato wart in North America is being carefully guarded and eradicated (61). The potato variety Aucklander Short-Top in New Zealand appears to be healthy, but carries a virus (25) that

is virulent on Arran Chief and other varieties, and that causes collapse of above-ground parts, as well as tuber decay. Tobacco, petunia, tomato and some other related plants are susceptible. The virus is said to be a strain of *Marmor dubium* Holmes.

A collection of 59 potato species and varieties taken to England from the Lake Titicaca region in Peru (35) was found to carry a number of viruses and virus complexes, several of them apparently new, that could be serious on our cultivated potatoes. A potato smut, *Polysaccopsis hieronymi* (Schroet.) P. Henn. (170), in South America, forms galls up to five centimeters long and half as thick on above-ground parts. The buba disease (*Thecaphora solani* Barrus), which ruins potato tubers in Venezuela (6, 7) and occurs in Ecuador and Peru, might be destructive here. *Heterodera rostochinensis* Wr. (27, 52), the golden nematode, so destructive to potatoes in Europe, has been found in a few hundred acres on Long Island, N. Y., where it is already reducing yields about 50%. It is hoped that studies under way will show that eradication of this nematode will be practicable.

Pea rust, *Uromyces pisi* (Pers.) D By. (59, 131, 146), occurs in several strains that affect *Lathyrus* spp. and other legumes, including garden peas. The alternate hosts are *Euphorbia* spp. This is an old rust and very troublesome at times in Europe unless control measures, including removal of alternate hosts, are maintained. Pea streak (Pisum virus 3) (24) causes heavy losses of garden peas in New Zealand, infections resulting in discoloration, cessation of growth and ultimate death of plants.

A grass rust, *Uromyces graminis* (Niessl.) Diet. (105), the alternate stage of which is common on fennel (*Foeniculum vulgare*), causes severe necrosis on carrot in Europe. This is a disease that is not usually destructive but might become so if introduced here.

A smut, *Urocystis brassicae* Mundkur (98), produces root galls on and greatly reduces seed formation by *Brassica campestris* var. *sarson,* an important oilseed plant. This smut also attacks radish, turnip, cabbage and related plants in India.

A root rot (*Zopfia rhizophila* Rabenh.) (30, 156) of asparagus is usually unimportant in Europe, but in 1935 it caused losses up to 80% in plantings in a German locality where it had not been noted since it was described from there in 1887.

Elsinoe batatas Viegas and Jenkins (73) sometimes causes a

serious stem and foliage scab of sweetpotato in Japan, Guam and Brazil.

A soft rot of squashes in Japan is caused by *Choanephoroidea cucurbitae* Miyake and Ito (91) which also rots flowers within a few hours after they become infected. Later the diseased flowers and fruits mummify.

Diseases of forage plants. A bacterial disease, *Aplanobacter rathayi* E. F. Sm. (38, 39, 122), is at times destructive to cocksfoot or orchard grass (*Dactylis glomerata*) in Europe and sometimes infects rye and one or two other grasses. The few seeds formed on infected plants carry the disease. Diseased seeds produce a poor stand, with distorted or stunted plants on which a gummy exudate glues infected parts together. In May 1945 this disease was found in a United States Department of Agriculture nursery at Corvallis, Ore., on plants of the Akoroa strain of cocksfoot grass grown from New Zealand seed.

The widespread rust of lespedeza in this country is *Uromyces lespedezae-procumbentis* (Schw.) Curt. (68, 69, 141) which does not infect oriental species of lespedeza even though those species are subject to severe attack by several strains of a rust called by the same name in Japan. These oriental strains and other oriental rusts of lespedeza have not been reported from North America.

A red clover disease, *Botrytis anthophila* Bond. (84, 120, 145), in Europe is spread from flower to flower by bees, and reduces seed yields. The mycelium grows under the seed coats of much of the seed that is formed and becomes systemic in plants grown from such seed.

A mosaic (3) due to a new virus which reduces spring growth of *Trifolium subterraneum* by 50% and affects other legumes, including peas, beans, soybeans, sweetclover and *Trifolium* spp., has been spreading rapidly in Australia and may be seed-borne.

Diseases of fiber plants. Leaf spotting and severe stunting of hemp (*Cannabis indica*) in Germany is caused by *Didymella arcuata* Roeder (113).

Flax rust (*Malampsora lini* (Pers.) Lév.) (137, 148, 154) is a serious disease in this country and necessitates the use of resistant varieties. Some of these resistant varieties are highly susceptible to strains of the rust that occur in Argentina. Other foreign strains occur in Germany, Australia and Tasmania.

Vein mosaic (31), a new virus disease, causes stunting of plants and distortion of leaves of species and varieties of cotton in Brazil. A cotton anthracnose, *Colletotrichum indicum* Dastur (33, 144), kills seedlings and ruins bolls in India. Infected seeds may germinate, but death usually occurs while seedlings are young. In infected soil all seedlings may be killed.

Diseases of forest and ornamental trees. A rust, *Cronartium flaccidum* (Alb. and Schwein.) Wint. (4, 15), which causes considerable damage to *Pinus sylvestris* in Europe, is potentially dangerous to our hard pines because its uredial and telial stages may be formed on a wide variety of hosts in several families, so that control by eradication of these alternate hosts would be extremely difficult or impracticable. Among these alternate hosts are peony, nasturtium and verbena. Uredia of the rust were found on *Impatiens balsamea* at the Experimental Farm, Charlottetown, Prince Edward Island, Canada, in 1925, but apparently the rust did not become established.

A number of rusts in this country attack needles or cause witches'-brooms on firs, but there are 50 or 60 additional rusts (67) of firs in various parts of the world that, as a group, have many alternate hosts. The combined effects of some of those species might well be destructive if they became established here.

A white heart rot due to *Polyporus litschaueri* (Lohw.) A. Bond. (13) infects 60% to 90% of the oak *Quercus mongolica* in the Russian Far East, often making the trees useless for timber. Elm, maple and poplar often are affected in various parts of Russia and Austria. A white rot of oak in Japan is caused by *Stereum hiugense* Imazeki (73).

A bacterial canker, *Pseudomonas fraxini* (N. A. Brown) Skor. (14, 121), causes severe dwarfing of a large portion of the ash trees in some areas in Europe.

Pestalotia disseminata Thuem. (58), formerly known from Portugal only, has recently been found doing considerable damage to young eucalyptus trees on the University grounds at Montevideo, Uruguay; a similar and perhaps identical species was found recently in the United States. Seedlings of several species of eucalyptus in Argentina were found to have chlorosis and stunting of the leaves, caused by a graft-transmissible virus (41).

An active leaf parasite, *Stegophora aemula* Syd. (140), on

Ulmus davidiana in China seems to be capable of causing serious injury to elms.

The well known and destructive watermark disease (*Bacterium salicis* Day) (34, 88) of willows in England has not yet been reported in this country.

A needle fall disease, *Exosporium deflectens* Karst. (115), of *Juniperus communis* in Finland and Rumania might be destructive here.

Leaves of *Acer trifidum* in Japan are killed by *Pseudomonas acernea* Ogawa (104) in such numbers as to seriously injure the trees and ruin their appearance. A number of species of maple are susceptible.

Diseases of ornamentals other than trees. The rose-wilt virus (*Marmor flaccumfaciens* Holmes) (55, 54, 70) is especially destructive on roses in Victoria, Australia, occurs in New Zealand, and is similar to a rose virus in Italy. Defoliation and death start at the tips of the plant and continue downward.

Carnation wilt (*Verticillium cinerescens* Wr.) (160, 161) has been destructive in England for a number of years.

A virus or a mixture of viruses (48) causing leaf curl and vein banding of *Ageratum conyzoides* and tobacco occurs in Ceylon. One or more new strains of virus capable of being serious if introduced are suspected of being involved.

A new virus leaf curl disease (82) of petunia occurring in South Africa was found to be transmissible to tobacco, tomato and other hosts.

A rust, *Puccinia distincta* McAlp. (64), is common on *Calendula officinalis, Bellis perennis* and *Senecio cruentus* in Australia and New Zealand. Infected plants are likely to be distorted or defoliated and ruined. In Japan, *Bacterium calendulae* Takimoto (142) is destructive to *C. officinalis,* especially among dense stands during rainy autumn weather, when it causes blackening and distortion of foliage and stems.

Snapdragon downy mildew (*Peronospora antirrhini* Schroet.) (100), first described on wild snapdragon (*Antirrhinum orontium*) in Germany in 1874 and later reported from Denmark and Switzerland, has recently been reported in Ireland (1936) and England (1937), where it has caused the destruction of large plantings of *A. majus,* the species grown in garden and greenhouse. The disease was found in New South Wales, Australia, in 1941.

Wild windflowers, *Anemone* spp., in Germany are badly distorted and ruined by a virus, *Galla anemones* Holmes (70, 77). Diseased plant parts in the soil carry the disease. How destructive the virus might be on related plants in cultivation is not known.

The destructive dahlia smut (*Entyloma dahliae* Syd.) (53, 83) is widely distributed over the world and has recently been found on a few plants in Oregon.

A leaf spot, *Cercosporella inconspicua* (Wint.) Hoehn. (93, 169), is a limiting factor in the growing of lilies in the Ukraine. The fungus is reported from elsewhere in Europe and from Japan.

In Africa wild *Gladiolus* spp. are severely injured by rusts (*Uromyces* spp.). A new rust, *Puccinia Mccleanii* Doidge (37), was recently described on *G. ludwigii* in South Africa.

Diseases of special or multiple-purpose plants. A rust, *Uromycladium tepperianum* (Sacc.) McAlp. (65, 128), sometimes destroys commercial plantings of *Acacia pycnatha* in Australia. The host is grown for tannin, perfume and gum, and is used as a sand binder. We do not know what the rust would do on acacias and related plants grown in North America.

Peanut rosette (*Marmor arachidis* Holmes) (124, 136) inhibits seed formation and is often destructive, crop losses being as high as 90% in some areas. It is reported from Java as well as from various parts of Africa. It is transmitted by *Aphis medicaginis* and perhaps other insects.

Soybeans grown in the Russian Far East are subject to destructive attacks by *Ascochyta sojaecola* Abramoff (2). A stem break caused by a *Fusarium* sp. (2) killed 9% to 22% of the young plants in the same area. In another part of Russia the *Fusarium* killed a large portion of the seedlings which were planted with seed from the Far East.

Lavender plantings in England are devastated by shab disease (*Phoma lavandulae* Gab.) (20, 57, 87) unless careful sanitation is practiced. Goosefoot (*Chenopodium album*), common as a weed in lavender plantings, is a host of the fungus.

A destructive root rot and wilt of pyrethrum (*Chrysanthemum cinerariaefolium*) on the island of Cherso, Italy, is caused by *Vialina radicicola* Curzi (32).

The oil and opium poppy and related forms are subject to a destructive seed-borne bacterial blight, *Bacillus papaveri* Christoff

(29, 36), in Bulgaria. *Pleospora calvescens* (Fr.) Tul. (28, 36, 112) causes drying out of poppy leaves and is especially destructive in Bulgaria. The fungus occurs elsewhere in Europe and in Japan.

A destructive leaf spot of tung trees in China is caused by *Mycosphaerella aleuritidis* (Miyake) Ou (108). It has been reported from Brazil, and a form of *Cercospora* found on tung trees in Florida may be the imperfect stage of this fungus.

The most severe damage to cork oak (*Quercus suber*) in Morocco is caused by *Hypoxylon sertatum* Dur. and Mont. (81) which starts on the outermost twigs and grows down to the trunk, after which the tree soon dies. The fungus has been reported on cork oak and walnut in Algeria and once on eucalyptus in Morocco.

Stevenson's manual (128), issued in 1926, lists several thousand diseases that are not established on the North American mainland, and numerous others have since been reported. Recently the present writer supplied plant-quarantine inspectors with revised and amplified notes regarding foreign diseases of some of our more important host plants. Over half of the approximately 1,700 pathogens and possible pathogens listed for the few hosts covered were not included in the manual. Doubtless the increase would have been greater but for the fact that in recent years world conditions have interfered with plant-disease studies and disrupted publication and receipt of such information. Some of the diseases mentioned in this paper are new, and only preliminary reports are available. None has been studied thoroughly enough to make it possible to predict with certainty its action on American-grown host varieties, under the varying conditions in North America, if or when it becomes established long enough to attain stabilized destructiveness.

GENERAL DISCUSSION AND CONCLUSIONS

Foreign plant diseases may enter with plants or products imported for food, feed or manufacturing purposes, or for propagation; with packing materials such as straw and rice hulls; or with bouquets or decorative plants. Pathogens may be present in or on these plant materials, and it may be impossible to detect them by a practicable method of inspection. Viruses are often carried by hosts in which no symptoms are produced at any time, as in some potato and raspberry diseases. Insect stowaways carrying viruses

may escape notice in bulk shipments which receive sample inspection only, or in merchandise or products which are not examined by quarantine inspectors. Oospores of downy mildews, and spores of rusts, smuts and other fungi, either individually or in leaf or stem fragments, are likely to be mixed with grain or other seeds from nearby plants as well as from infected hosts. Infected sugarcane is often planted. Potato tubers infected with virus or tuber rots, or contaminated by adhering fungus spores, bacteria or nematodes are used for planting purposes. It is necessary to know something of the methods of reproduction of a pathogen and the possibility of its occurrence in viable condition in, on, or with the parts of the host that are imported in order to appraise the likelihood of its entry. The evidence is clear that many destructive plant pathogens have been and others may be spread with plants and plant parts or products as imported. The greater speed of transportation and improved conditions of storage in transit greatly increase the likelihood of undetected importation and ultimate establishment of foreign pathogens[3].

It is obvious that destructive foreign diseases abound; that they are of many types, not only as to their taxonomic positions, but as to the hosts and host parts affected, their effects on the hosts, their modes of spread and survival, preferred ecological conditions, methods of control, and possible methods of entry; and hence that preventing their entry for as long as possible and mitigating the effects of their entry are difficult and complicated problems. Every useful plant is entitled to the maximum protection that is profitable; all of us receive direct or indirect benefit from such plants and are entitled to have our interests protected.

Needed protection may be attained by maintaining a planned program to include the following:

(*a*) Thorough study of foreign plant diseases so that we may know what they are; how they grow, survive and spread; how they affect all parts of their hosts; what varieties they attack; how they can be detected on material destined for this country; and how they can be eliminated therefrom.

(*b*) Use of quarantines drawn on the basis of biologic and economic facts, use of the most highly developed techniques for inspection and treatment of incoming plant material, including, when

[3] *See* McCubbin, W. A. Preventing plant disease introduction. Bot. Rev. **12**: 101–139. 1946.

desirable, growth of propagation material under observation until found to be disease-free.

(*c*) Use of plant disease surveys to find diseases before they can become widely or perhaps permanently established, and thus to make possible their early eradication.

(*d*) Development of eradication methods for different types of diseases, crops and conditions, so that eradication may be effected promptly and economically, if practicable.

(*e*) Development of control measures, including good resistant varieties or breeding stocks, in anticipation of possible establishment of destructive foreign plant diseases that are likely to be introduced.

In general, we should obtain the data needed and then take the steps necessary to protect ourselves efficiently and effectively from needless economic and esthetic losses of plants and plant products through the ravages that otherwise will follow the inevitable arrival of destructive plant diseases not yet established in North America.

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MARINE ALGAL ECOLOGY

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INTRODUCTION

The ecology of marine algae has now reached a stage, marked by the accumulation of a considerable volume of literature, where some attempt at integration is desirable. Plant and animal ecologists have generally pursued somewhat different paths, but it is impossible for the marine algal ecologist not to take cognizance of the work of his zoological co-workers. It is of course possible to carry out marine algal studies without regard to the associated animals, but such work can be regarded only as incomplete. The necessity to consider both plants and animals (46) has rendered the subject fraught with more difficulties than it would otherwise possess, but it is impossible to avoid them. It is hoped that some of these difficulties will become apparent in the following pages.

It is convenient to commence with a brief summary of the more important descriptive or synecological studies, since these, from a chronological point, were first in the sequence; only later did autecological studies make their appearance. Generally speaking, marine algal ecology is still in the synecological stage, and autecological studies are only just beginning to appear.

It has been evident for some time that algal communities on sea shores can be grouped into certain broad regions, each of which is most suitably regarded as a whole. Thus the Atlantic, Arctic and North Sea coasts of Europe are akin in their vegetation with the shores of Iceland and eastern North America. Similarly the coasts of western North America, Japan and Siberia form another entity. Both these major areas are characterised by predominance of large brown algae belonging to the Laminariales or Fucales. In tropical and subtropical warm waters brown algae cease to be so important and the Rhodophyceae are more conspicuous. In the warm waters one may distinguish four more important regions—Caribbean, Mediterranean, Indo-Malay, Central Pacific—whilst there may be other smaller units. In the colder waters of the southern hemisphere we again encounter an area where the larger brown algae predominate. At least two major separate regions can be distinguished

there, South America and New Zealand. Although the larger brown algae predominate in the floras of northern and southern cold waters, nevertheless their aspect is very different in the two regions because the species are commonly totally distinct. One may also observe that in colder regions the littoral[1] vegetation is extremely well developed, whereas in warmer waters it is the sublittoral that is more luxuriant. Conditions in the littoral militate against survival of delicate algae during periods of low tides in the tropics and subtropics, and hence the vegetation tends to be poorer in number of individuals and of species. There is also the seasonal fluctuation in the algal vegetation. Thus in the north temperate region the algal flora is at its height in July and August, but in the Mediterranean it is at its best during winter and spring, though the sublittoral is maximal in summer when the littoral is strongly reduced.

In the north and south temperate regions the flora has frequently been studied in relation to the nature of the coastline (49). Thus one can consider the vegetation of rocky shores (exposed or protected from wave action), estuaries, sandy shores, muddy shores and salt marshes. A similar classification can also be employed for tropical vegetation, except that mangrove swamps occur in many of the areas that otherwise would be salt marsh. Because of their peculiar nature and also because of differences in their environmental factors it is desirable to consider independently the rock pools of rocky shores and the salt pans of salt marshes. Most of what immediately follows applies principally to the algal ecology of rocky shores (74).

ATLANTIC EUROPE—EASTERN NORTH AMERICA

A considerable volume of work has been published dealing with the algal vegetation of this region (1, 5, 8, 10, 21, 22, 27, 34, 42, 44, 46, 49, 53, 56, 70, 73, 84, 85, 88, 90, 91, 97, 101, 102, 109, 115, 116–119, 123, 125, 126, 128, 139, 145, 149, 151, 152, 156, 177, 185, 189, 191, 192, 194, 196–199, 206, 208, 224, 225, 226, 228, 262, 263). The number of communities recognised has depended partly upon personal predilections and partly upon the amount of time expended upon a survey: the longer the time the greater the number of communities usually described.

[1] For definition of the Littoral, cf. p. 654.

At the outset certain important conclusions can be drawn. Thus, it is very evident that the zonation to be observed in chalk areas (1) differs markedly from that of other regions, whilst the vegetation of the Baltic (145) also exhibits peculiarities based upon its tideless nature and gradients in salinity. Another feature is the part played by ice formation in the Arctic and Antarctic, and also the Baltic, in preventing some species from growing on the littoral (232).

Many of the communities described from the different shores are not of equal ecological status, and this renders any attempt at comparison extremely difficult. If future workers accept normal ecological practice as the basis of their nomenclature it will greatly facilitate comparisons of floras from different areas. One attempt at equating the different algal communities on British shores has been made (38), and it seems clear that there is a more or less basic zonation which can be found in the majority of localities. The very top zone in the spray area is generally dominated by *Hildenbrandtia* and *Verrucaria;* below this at about E.H.W.M.S.T.[2] there is often an upper *Enteromorpha* belt, usually with other associated Chlorophyceae, or alternatively a *Porphyra* belt with *Bangia* and *Urospora.* Then comes a zone covered with plants of *Pelvetia canaliculata* followed further down by *Fucus spiralis* or its variety *platycarpus.* The next two successive plant belts vary in their position according to local factors so that the balance between the two species *Fucus vesiculosus* and *Ascophyllum nodosum* must be very delicate, and indeed in many areas they commonly occur as a mixed community. The next lowest fucoid zone, near L.W.S.T., is dominated by *Fucus serratus,* though in certain exposed areas one may find all these lower belts replaced by a single zone of *Himanthalia lorea* (73) or a *Gigartina-Chondrus* community. Farther north, *e.g.,* the Shetlands, slight changes occur in the basic zonation (21); *e.g., Fucus serratus* is absent, but minor changes of this category occur elsewhere (109). Around M.L.W.S.T. one frequently finds also a lower *Porphyra* community and a *Laurencia* community. In the sublittoral *Laminaria digitata* commonly forms the uppermost belt and it is usually succeeded, at two to three fathoms, by *L. cloustoni,* the lower limits of which are extremely variable. It is said to be determined principally by the degree of

[2] Extreme High Water Mark Spring Tides.

light penetration (77), but there is little doubt that complex interactions are also involved.

The vertical extent of the zones on any shore is directly correlated with the angle of slope of the beach and the extent of the tidal rise. This latter effect is very pronounced and can be demonstrated by a comparison of zonations from different areas (34, 264). The zonation in any area may vary during the seasons (123), and this is also a fact which must be taken into consideration though it is one that has not received as much attention as it deserves.[3]

NORTH PACIFIC

This area has been little studied ecologically, apart from an investigation into the distribution of the great kelp beds (31) and an analysis of the geographical elements (179, 217). There is no doubt that in it a very fruitful and profitable field is still awaiting investigation. Future work will probably have to be based to some extent upon that of zoologists (2, 223), though it is probable that a new approach will be necessary because too much insistence has been placed upon the rôle of animals. So far four biomes have been recognised, all dominated by animals, and even the great kelp communities are treated only as associations or fasciations of the animal formations. It seems clear that a combined approach by both zoologist and botanist should do much to determine the effective status of the different communities.

SOUTH PACIFIC

New Zealand. The nature and composition of the algal communities in these cold waters differ from those of the northern hemisphere. The area is very rich, but so far only a few ecological studies have appeared. In one of these (180) eight formations were recognised, each comprising a number of subformations and associations characterised principally by either algae or animals but not by both. Later work (50) has rectified this outlook and shown that very often the animals and plants should be regarded as co-dominant. A spray zone can be present, but no data are provided of its extent. It is perhaps significant that the two principal marine ecological studies from this area have been based upon the biotic

[3] A seasonal succession is as follows (151): Oct.: barren; Nov. to Jan.: *Ilea-Scytosiphon-Dumontia-Polysiphonia;* Feb. to Ap.: *Monostroma-Spongomorpha-Bangia;* May, June: *Laminaria-Chorda-Polysiphonia;* June: *Chordaria;* Aug. to Sept.: clearance of all annuals.

concept of natural communities (biomes). A definite zonation of both plants and animals has been described, the principal communities being briefly as follows: above H. W. M. in the spray zone there is a *Verrucaria* and Cyanophyceae belt, whilst the top of the littoral is occupied by *Chthalamus;* below this the sequence is first an *Apophloea-Elminius* association, then a *Novastoa*-encrusting coralline association, and finally a belt of *Xiphophora* and *Carpophyllum elongatum;* in the sublittoral there is a Rhodophyceae association, a *Lessonia* association and in places a *Macrocystis* association; these may all be displaced downwards to some extent in areas where there are both shade and tumultuous waters.

South America and the Antarctic. Our information about the algal ecology of this region is extremely meagre and is largely based upon the work of a single contributor (230–232), though there are, of course, a number of flora lists. There is, therefore, a vast potential field that requires intensive study, and there is now a sound basis upon which further work in subantarctic and antarctic waters can be built. Some of the formations described will need modification, and zoologists will have to contribute their quota in order to complete the picture. A large number of associations within the formations have been recognised, and, as may be expected, there is a marked difference between protected and exposed coasts. One of the more outstanding features is the very large number of communities described from the sublittoral, a condition reminiscent of the tropics. The littoral vegetation is relatively poor in communities, due to ice removing many of the plants and so preventing a number of the perennials from becoming established.

Throughout the South Pacific there is a marked absence of dominant fucoids in the principal zonations, though *Hormosira banksii* may play a subsidiary rôle in New Zealand, whilst on exposed coasts *Durvillea antarctica* sometimes forms a community near low water mark. The subantarctic sublittoral is characterised by associations of the giant kelps (*Lessonia* spp., *Macrocystis pyrifera, Durvillea harveyi*) but these are unable to penetrate into the even colder waters of the antarctic where *Desmarestia, Leptosarca* and species of Rhodophyceae form associations that have yet to be studied in detail.

SOUTH ATLANTIC

We owe our knowledge of this region mainly to the series of excellent works (30, 61–63, 107, 146, 169, 236, 237, 240, 241) on

the South African inter-tidal zone. These have been summarized (236, 237) in order to emphasise the general picture. It is clear that this type of investigation, in which a large area is selected and studied over a long period of years, will yield important results and information of the greatest value, and co-operative work such as this should become the rule rather than the exception. The vegetation of the shores varies in passing from the warm waters of the east coast round the south coast to the cold waters of the west coast, and the transitions from the two extreme zonations on west and east have been carefully traced. This change in zonation is dependent very largely upon the temperature relations of the various species. Apart from the principal changes in the zonation there are also local changes associated with the exposure or protection of the coast (237).

On all three coasts there is a well marked upper *Littorina* belt, though certain associated species become more abundant on the warmer east coast. Below is an extensive balanoid zone which is less thickly populated on the west coast. The lower part of this zone is occupied by *Patella argenvillei* on the west coast, but on the south coast it is represented by a distinct *Patella cochlear* belt. On the east coast both species of *Patella* gradually disappear and are replaced by a carpet of red algae. The lowest zone, or sub-littoral fringe as it is called, is mainly composed of Rhodophyceae on the east coast, whereas on the south coast it is dominated by the crinoid *Pyura* and in a few places by *Macrocystis pyrifera*.

It will be seen from this brief account that there is a relatively simple basic zonation which, it is believed, can be applied to other areas (236) outside South Africa, *e.g.*, Scotland, where it is possible to demonstrate an upper *Littorina* zone and a lower balanoid zone, together with a sub-littoral fringe. Terminologically the name sub-littoral fringe is hardly satisfactory, and since it varies so widely in composition from place to place future work is likely to necessitate its division into formations and associations. Additional studies will also be necessary before it can finally be accepted that the *Littorina* and balanoid zones have an extensive distribution. In view of the fundamental differences between the algal vegetation of the northern and southern hemispheres it is doubtful that the relative insignificance attached (236) to the fucoids in northern waters is justified.

CARIBBEAN REGION

Ecologically this area has been but little studied, although lists of the marine algae to be found in parts of it are in existence (20, 23–25), whilst there is a fairly extensive study of the algal associations and facies of the Azores (207), which can be included in this region. There is reason to believe that lime-depositing Cyanophyceae may play some part in the building up of the shore line (18), though not perhaps to the extent they do elsewhere. In spite of the extremely small tidal range of the area one can find perfect examples of algal zonation, albeit on a reduced scale (41), and there is no doubt that a big field awaits investigators both here and in the following region.

INDO-PACIFIC REGION

(Including Oceania and tropical Eastern Australia)

A little information is available about algal zonation on a Ceylonese reef (244), on the Great Barrier Reef (239) and also on Hawaii (153) and Tahiti (216). This region and the previous one suffer from the fact that most of the work has been carried out by visiting scientists, and no real advance in their ecology is likely to be made until workers who are resident in the tropics inaugurate some investigations.

THE MEDITERRANEAN

This area is fortunate in possessing a well equipped marine station at Naples and also in having suitably located Universities. In addition, the shores are readily accessible to workers from other European Universities during summer vacations. As a result, a number of ecological investigations of very high value (12, 60, 64–67, 147, 181, 187, 204, 205, 209, 218–220) have been forthcoming. In some of these the biotic concept has been adopted as a basis for description of the communities, but the majority of the investigators have been concerned either with plants or with animals.

A very large number of associations have been recognised, though many of them would not enjoy this status if proper ecological terminology were applied. In the supralittoral seven communities have been recognised at Albères including *Verrucaria* and *Hildenbrandtia* (66). The number and nature of the littoral communities depends on whether the coast is exposed or sheltered, but in either

event there is a lack of dominant fucoids, and their place is occupied by *Bangia, Porphyra, Rissoella, Tenarea, Nemoderma, Corallina, Ralfsia, Cladophora, etc.* As might be expected in warm waters, the number of communities to be recognised in the sublittoral is large, no less than 12 in one case (66). The most characteristic feature of the sublittoral is the presence of a number of communities, each dominated by a species of *Cystoseira.* Areas with muddy or sandy bottoms are dominated by marine phanerogams, a group which tends to play a much larger part in the ecology of warmer waters. Different profiles (66) have been used to illustrate the variations of zonation that can be found under varying conditions of slope, shade and aspect. There is no doubt that the Mediterranean represents the most fully studied warm water region, and some effort should now be made to bring our knowledge in tropical regions up to the same degree of excellence.

One of the problems up to the present has been the difficulty inherent in preparing an accurate survey of sublittoral vegetation. The exigencies of two successive wars, because of the commercial value of oarweeds and giant kelps, have done something to stimulate research. Between 1912 and 1914 a detailed survey was undertaken of the kelp beds of the Pacific Coast of North America (31), the work mainly being carried out by means of surface craft. Similar methods have been employed during the present war to survey the *Macrocystis* beds around New Zealand (188), but very different techniques have had to be introduced in order to survey the submerged *Laminaria* beds of Great Britain (40), and the use of the echo-sounder and aerial photography may mark a new era in algal ecology. In some cases it is even possible that differences in rockweed vegetation can be seen by air photography, but further research will be necessary in order to show whether any use can be made of these two techniques in warm waters. Using these methods large areas can be surveyed and mapped in a relatively short time, and as a result it has been found that the lower limit of *Laminaria cloustoni* is not uniform around Scotland. This fact, when considered in the light of our knowledge of the physiology of the alga[4] and the different types of environment in which it occurs, can illuminate certain ecological problems; and if it does not succeed in providing a complete solution, it nevertheless certainly

[4] There are three physiological races of this species (160).

indicates the lines along which a solution should be sought, not only for this species but also for others.

ROCK POOLS, CAVES, SALT MARSHES AND PLANKTON

The vegetation of rock pools has received little attention, and there is plenty of scope for additional work. The flora of pools in various areas has been described (13, 49, 52, 54, 66, 88, 99, 109, 112, 120, 134, 191, 229, *etc.*), and certain differences noted as compared with the remainder of the beach vegetation. Hence much of the flora is transient (11), and there is often a microzonation around the walls of the pool. Three different types of rock pool have been recognised (66, 88), depending on their vertical elevation on the shore. These three categories are: *a*) sublittoral pools characterised by protection from surf and water currents, *b*) littoral pools, *c*) supralittoral pools of the spray and supralittoral zones. This last group often has a layer of fresh or brackish water floating on top of the denser salt water, and they may also contain peculiar forms of well known species (*e.g., Enteromorpha* at Nahant, Mass., and *Fucus serratus* in the Orkneys found by the writer). The conditions in these three types of pool are very different, but more data are required in order to place these differences on a quantitative basis. Some attempt in this direction has indeed been made for pH and temperature variations (120) where a gradation was recorded from pools dominated by Chlorophyceae and showing considerable fluctuations to pools dominated by Rhodophyceae with very small fluctuations.

Various authors (15, 49, 52, 120, 134–137, 229) have made suggestions concerning the nature of the factors that control the vegetation in these pools, and the following seem to secure general agreement: *a*) height of pool on shore, *b*) depth of water in pool, *c*) size of pool, *d*) drainage action of surrounding algae, *e*) isolation, *f*) temperature changes, though this may affect certain species only (15), *g*) salinity changes, *h*) biotic interactions, *i*) light penetration. pH is not regarded as a limiting factor (15, 119) because the majority of algae will tolerate a very wide range, but slope may affect the density of the cover (229). Although the above list may seem imposing, much of the work has been empirical, and there is still scope for further intensive study.

The elements composing the flora of rock pools have been seri-

ously studied in only one locality (13) where it was found that there were four components: *a*) species characteristic of the sublittoral, *b*) species from the ebb line that reach their upper limit on the beach in the pools, *c*) littoral species, *d*) species wholly confined to pools. One interesting feature is the discovery that algae from tide pools have a greater range of osmotic tolerance than species from the sublittoral, but this is perhaps to be expected, since salinity changes in rock pools may be very considerable.

The ecology of cave vegetation has received some attention (1, 49, 133, 134, 141), but additional data will be of considerable value. Shade species are common on the walls of caves, and certain forms are capable of penetrating a considerable distance into a cave. The ultimate limit of penetration is set by the amount of light within the cave. Both micro- and macro-climates are considerably different in a cave as compared with the rocks outside, and this naturally exerts an effect on the vegetation. Some information is available about these factors (92, 133, 134), and it seems that light and humidity are probably the two most important.

On salt marshes the pans correspond to the rock pools of rocky shores and to the sand pools (49) of sandy shores. Much of the pan vegetation is transient and adventive, but there is no doubt that a definite pan flora can be recognised (34, 37–39). Our information concerning this flora is at present extremely meagre because it is a habitat that has been neglected by ecologists, although it is very suitably circumscribed for ecological study. Similarly our knowledge of the environmental conditions in such places is almost lamentable, although it is known that there are great changes in salinity and temperature and that these may occur at different depths in the pans (174). During the summer pans on the upper marshes may dry out (37), and then the concentration of salt rises until it crystallises out on the soil. The oxygen and pH factors are, as might be expected, controlled by the amount of animal and plant life present (174).

Some of the species that occur in salt pans are somewhat unexpected because they are more typical of rocky shores. In the pans they grow attached to the mud banks or to the exposed roots of phanerogams (34). Examples of such species are *Colpomenia sinuosa, Striaria attenuata, Polysiphonia fibrata, P. elongata* and *Myriotrichia filiformis.*

On the salt marshes proper fewer ecological studies of the algae have been attempted than on rocky shores (38). Well marked communities can be and have been distinguished (32, 34, 36, 37, 49, 110, 177, 191), and suggestions have already been made for coordination of nomenclature on a proper ecological basis (34). So far only the algae of salt marshes on the Atlantic or North Sea coasts of the northern hemisphere have been investigated in any detail, and it is noticeable that there is a general similarity in their floras. One of the most interesting features of the salt marshes is the presence of free-living or embedded marsh fucoids (7, 32, 34–37, 49, 85, 131, 145, 150, 233, 234). These have originated from normal attached forms, but in some cases they have become exceedingly modified. All the common littoral fucoids, including *Fucus serratus* (173) and *F. ceranoides,* appear to have given rise to these free-living forms, though their origin has by no means been satisfactorily elucidated and the distribution of the different types on salt marshes has yet to be worked out thoroughly. One of the more interesting recent discoveries is that of the existence of a comparable free-living form of *Macrocystis* (265), but at present there is very little information about its environment.

The distribution of the various algal communities in time and space (32, 37) brings out interesting features, illustrating not only the seral nature of some of the communities but also their relationship to physiographic features of the salt marsh or to the phanerogams. Cyanophyceae are often pioneers on the lower mud flats, and they are also more common on the upper marshes where their gelatinous nature protects them during long periods of desiccation (37). A comparison of the vertical distribution of species common to salt marsh and rocky coast shows that very often there may be divergences which provide a clue to the factors controlling their distribution (37).

The field of salt marsh algal ecology has barely been broached as yet, and it is to be hoped that future workers will not neglect it as in the past. Even more seriously neglected is the algal ecology of the tropical counterpart of salt marshes, mangrove swamps. Not only do new species probably remain to be discovered from such habitats, but at present we know nothing about the vegetation with any degree of completeness (68). At least one very peculiar plant has been recorded (251) from the Indo-Malayan mangrove forests.

It is barely possible to embark upon the ever-growing body of literature concerning the ecology of plankton. One of the more striking features is the dominance of Cyanophyceae in warmer waters (77), whilst the relationships between planktonic algae and food fish are slowly being elucidated (202). Plankton, however, forms a topic which demands separate treatment; hence no further details will be given here.

ENVIRONMENTAL FACTORS

The geographical distribution of the majority of algal species is controlled by temperature (108, 211–214), often in relation to the production of fruiting organs (*e.g.,* Laminariaceae), many species tolerating only a narrow range. Thus in the Adriatic the distribution of *Fucus virsoides* is controlled in this manner, the plants gradually becoming smaller towards the south and finally disappearing as the mean average sea temperature rises (205). One result of this type of relationship is that the same species occurring in different areas may flourish at quite different periods, *e.g.,* some Mediterranean winter species occur as summer species in the English Channel (66). However, this correlation between resistance to warmth and distribution does not always exist (16), and it is therefore evident that each species must be investigated individually. Apart from this principal temperature relation the distribution of algal species may be controlled locally by the operation of other factors (200); thus in the Baltic lack of tidal movement and salinity gradients are of considerable importance (145). In such land-locked areas it is customary to find a reduction not only in the total number of species but also in the size of the actual plants. In the Arctic and Antarctic the shore vegetation is restricted to species that can survive freezing and ice action every winter (232). It is, however, somewhat surprising that there are very few annual species in these two regions. The above are probably the main factors controlling geographic distribution, though others may function locally (129), but the presence or absence of a species in any given area is largely dependent upon the existence of a suitable substrate; *e.g.,* kelps will not be found in abundance where there is a sandy bottom, whilst the vegetation of chalk is very different to that of a granitic or felspar coast (1, 34).

The vertical zonation of plants and animals that can be observed

on most of the rocky shores of the world has stimulated many investigations in order to determine the factors responsible for the phenomenon. In a recent symposium (39, 46, 55, 238) certain aspects were examined and it was generally concluded that although we are approaching some understanding of the primary causes, the picture as yet is far from complete.

It would seem that there are three groups of factors operating on a rocky shore: firstly there are those which actually determine the upper and lower limits and which can be termed the causal factors; secondly there are those which determine whether a given zone shall be present or absent in a locality, *e.g.,* heavy wave action: these may be called presence or absence factors; thirdly there are the *modifying* factors which are responsible for modifying the breadth or vertical position of a zone, *e.g.,* spray or seasonal temperature changes.

Locally along European shores severe wave action may act as a presence or absence factor in eliminating *Ascophyllum nodosum* and *Fucus vesiculosus,* whilst a sand covering on the rocks results in the introduction of a number of other species, *e.g., Sphacelaria radicans* (49); a small rivulet of fresh water may break up the fucoid zonation completely and replace it by a vertical zone of *Enteromorpha* and *Cladophora,* though if the stream is large enough *Fucus ceranoides* may replace the other fucoids. Generally speaking, normal variations in concentrations of nutrient salts are not important, but an increase of nitrogen in the vicinity of sewage outflows results in the development of an abundant chlorophycean flora (*Ulva* and *Enteromorpha* (48)).

It is often easy to note the operation of local factors, and though the majority of investigators (6, 12, 49, 56, 80, 85, 91, 168, 264) are agreed that in the littoral zone the principal causal factor is exposure, at present there is no agreement as to how exposure operates or should be measured. On European coasts it is at the upper limits, where conditions are extreme, that one can find species (*Bangia fusco-purpurea, Urospora penicillus*) that can tolerate very high temperatures and severe drying. Exposure of the seaweed thallus to the air permits it to undergo considerable water loss (91, 104, 105), and in temperate regions this is probably an important limiting factor. In the tropics the heating of the thallus to a temperature that might kill the protoplasm, certainly of more deli-

cate species, may be more important than the water loss, though there are some red algae (*Rhodomela crassicaulis*) which do not suffer damage from this (77). It is not yet established whether water loss acts directly, because as the water is lost, the salinity of the surrounding medium and also the osmotic pressure of the cell sap rises, and this may be the ultimate factor (13, 14) at higher levels on the shore, although the osmotic pressure in certain species is dependent upon the wave length of the light (16). The algae so far studied fall into one of three groups so far as resistance to changes of osmotic pressure are concerned, and their grouping is directly related to their vertical position in relation to mean sea level. There is no doubt that each species will have to be investigated individually because it is extremely unlikely that a common causal factor controls the vertical distribution of all the littoral species.

So far as measurement is concerned, exposure can be estimated in terms of hours of submergence or emergence or the ratio of the one to the other. This type of relationship has been worked out for at least three localities (45, 91, 110). At this point, however, one must distinguish between inter-tidal and non-tidal (39) exposure, and it is probable that the maximum periods of the latter (which may extend into numbers of days, especially in the summer) are of far more significance than the former. Unfortunately this factor has been studied only on salt marshes, and no doubt when it comes to be investigated on a rocky shore it will provide some very significant results. Another aspect of desiccation that will certainly prove to be more important than any so far studied is its relationship to the establishment of sporelings. We know very little about the response of sporelings to varying degrees of exposure, yet it must be at this stage or at germination, rather than at the adult stage, that control of zonation is effected. One or two workers (12, 28) have indeed drawn attention to this aspect, but no adequate data are as yet available, possibly due to the very real difficulty of identifying sporelings accurately at an early stage. We may say that exposure in a general sense can be regarded as one of the prime causal factors, especially in determining the upper limit of species.

The tidal phenomena associated with a littoral beach vary considerably with height on the beach, and attempts (45, 52) have been made to ascertain whether there are not certain critical levels

which mark the upper or lower boundaries of the majority of species on the shore. There is no doubt that this method of approach is likely to lead to important results, but until data from more areas are forthcoming it is difficult to assess the probable outcome. The inherent difficulties can be appreciated when we note that the two workers who have approached the problem from this angle recorded only one critical level that was common to both areas. The analysis can perhaps be carried somewhat further by equating weed zones from different localities to a common basis, *e.g.*, the tide (39, 264). This operation shows that the algal zones do not always bear the same relation to the tidal levels in the different localities, but it also suggests that for the fucoids there may indeed be three critical levels. If the problem is attacked along similar lines in other areas there is little doubt that some substantial progress will be made.

Of the other factors that operate throughout the littoral the mechanical effect of the waves is likely to be a presence or absence factor, affecting both abundance and composition of the flora. Certain species require the vigorous aeration associated with surf, *e.g.*, *Postelsia* (216, 235) and *Valonia* (242), whereas others do not. On the other hand, the velocity of the tidal current during ebb and flow may be a causal factor, though further investigation is desirable. There is usually little or no current around high or low water, and the maximum current is usually between the third and fourth hours of rise or ebb. It is a fact that in many areas *Ascophyllum nodosum* and *Fucus vesiculosus* occupy this zone that is associated with rapid movement (39, 52, 59), though whether the lower limit of *F. spiralis* and the upper limit of *F. serratus* are also related to these movements has yet to be established.

It has already been pointed out that the geological nature of the rock may behave as a presence or absence factor, but the angle of slope may act similarly or as a modifying factor in enabling, through shade, a zone to be elevated slightly. Slope is also important in connection with the rate of drainage and hence of desiccation, but this has scarcely been worked out in any quantitative manner.

Spray acts as a modifying factor in that it may elevate some of the upper zones (45), whilst the actual extent of the tidal rise also operates similarly in that it controls the vertical extent of the zones

on the shore. Temperature acts in a similar way because seasonal migrations of species that form distinct belts have been recorded (123, 165). In temperate regions exposure to unfavourable low temperatures may also produce a temporary modification in the zonation, but it is dependent upon a low tide coinciding with a severe frost (39, 52, 127).

Several workers (12, 57, 82, 222, 230) have suggested that light may be an important causal factor, and in extremely silty areas this may be so, whilst for *Fucus evanescens* (82) there is evidence that young plants soon sicken and die if the light intensity is reduced. Temperature, light and salt concentration may all influence germination of *Fucus* oospores (122) and this type of investigation wants extending so as to include other genera. Further work is needed on this factor in spite of the tendency to discount it during the last decade or so. We now know that many algae behave either as sun or shade forms (137, 162, 163, 221), and this fundamental physiological distinction may underlie some of the zonations. Some of the fucoids bear bladders, *e.g., Fucus vesiculosus* and *Ascophyllum nodosum,* and when these plants are submerged the fronds float (96). This flotation of the fronds will materially modify the light factor, but quite apart from any such modification there is some evidence that in *Ascophyllum* the hydrostatic pressure of the bladders may be a factor modifying the lower limit of this species (51).

The relation between assimilation, respiration and littoral zonation is a problem that has only recently commenced to be explored (57, 82, 102, 121, 124, 159), but the higher the alga grows on the shore the shorter the time available for metabolism and growth, and when this factor can be translated into suitable terms it will probably prove to be a causal factor of first importance. It has already been shown that considerable photosynthetic gain is possible during periods of exposure (243), and that algae respond in three ways in respect of the effect of water loss on assimilation and growth (114). The results so far obtained for the relation of photosynthesis and respiration to changes of salinity (154) are somewhat conflicting. Thus a reduction in the salinity increases the rate of photosynthesis in *Fucus serratus* and *Ulva lactuca* (144), though the reverse has also been reported for *Ulva* (77). Reduction also increases the rate of respiration in *Fucus serratus* and

Laminaria digitata, whereas *Fucus vesiculosus, Enteromorpha* sp. and *Porphyra* sp. are not affected (100). The exact status to be allotted to the animals in their effects on the zonation has yet to be worked out in detail, although this aspect has not been wholly neglected (45, 116–118, 236, 237, 250, 255); at present there is still some divergence between botanist and zoologist (238). It is, however, very doubtful that many workers would subscribe to the view that the biotic factor is a master factor (194). As marine co-operative research becomes the rule rather than the exception this aspect should become clarified.

In summing up the position it seems that the evidence is more promising with regard to the determination of the upper limits of species, and at present it is very difficult to suggest factors that control the lower limits. It is doubtful that any weight can be attached to the suggestion (87, 122) that at lower levels increases of salt concentration are significant, though so far as green algae are concerned it seems that the concentration of sea water is the optimal one for their assimilation (78) . The lower the position on the shore the more favourable the environment becomes for the growth of seaweeds, and it may be competition between species for space and light that is the essential causal factor at lower levels. Here the comparative rates of growth and reproduction of the different species will be important, and also the effect of epiphytes, but our knowledge of these factors is hardly extensive. In general, variations in pH do not seem to be important, though in one species of *Fucus* successful growth of the sporeling takes place only over a relatively narrow range (81); this aspect demands further enquiry. The view that the upper limit of *Laminaria digitata* is correlated with the superficial position of sporangia and their exposure to water loss, and also that the lower limit of *Fucus serratus* is set by the thallus being unable to contract sufficiently to force gametes to the surface (105), can scarcely be entertained, since it is obvious that unless the sporelings can grow, neither of these two conditions can be involved. The power of species to resist desiccation decreases the lower they grow (6, 167), but this, in the case of the fucoids, appears to be bound up with the microchemistry and microstructure of the cell wall (93, 264): the lower the species on the shore the thinner are the cell walls and the less the amount of fat they contain.

So far, only the factors controlling littoral zonation have been considered. For the sublittoral there is general, though not universal, agreement that light penetration is the prime causal factor. This operates in its effects on assimilation rate, and this has also to be related to respiration (43, 57, 58, 82, 114, 121, 141, 160–164, 171, 221, 222). A critical depth for any species is obviously that where assimilation becomes equal to respiration (the compensation point). This depth for any species may be modified indirectly by the effect of such external factors as wind, which makes the water rough, and clouds (57, 222, 252). Below the compensation point depth, wear is not wholly replaceable, and it is not improbable that the depth varies with the age of the plant; at present we do not know how it may also vary from season to season and from locality to locality.

So far as actual light absorption is concerned it would appear that the colour of the alga acts in a physical rather than in a physiological manner (163, 221), and in this particular respect the distinction into sun and shade algae is of very considerable importance. The inter-relationships, however, may be distinctly complicated: thus red algae from well lit habitats (sun forms) in deep water possess no advantage over shade Chlorophyceae; similarly, Rhodophyceae and Phaeophyceae from the same horizon do not differ much in their capacity for photosynthesis. The recent discovery that *Laminaria cloustoni* exists in three physiological races, sun form, shade form and deep-water form, alters our concept of its behaviour around our coasts. The lower limit to which the species extends in any locality will depend on the physiological form present. This is a problem that no one has yet attempted to survey and solve.

The correlations between light penetration, absorption, assimilation, salinity and temperature are only just beginning to be worked out, and it is evident that the results (58, 102, 130, 172) may throw considerable light not only on the zonation to be observed in any one locality but also upon the geographical distribution of the species. There already appears to be some correlation between the temperature giving maximum assimilation and the average temperature during the month of maximum growth (58), whilst the great development of fucoids in the Arctic is probably due to the indirect effect of lowering the temperature, thus leading to an

excess of assimilation over respiration (102). The fact that some algal growth can take place in temperate waters during winter and spring is due to the low respiration rate, so that in spite of the low light intensity assimilatory gain is possible (186). Latitude is also said to be significant because in the warm seas the compensation point is reached sooner with depth, but this result hardly tallies with the fact that the algal vegetation of warm water often descends to a greater depth than that of cold.

Whilst light may be the main causal factor in controlling the sub-littoral zonation, there are other presence and absence or modifying factors. Changes in the substrate will act as a presence or absence factor, whilst the existence of a strong swell, *e.g.,* the Pacific coast of North America, or of strong currents, *e.g.,* around the Orkney Islands, results in the extension of the large Phaeophyceae to greater depths. This factor must operate through increasing either the aeration, and hence respiration and assimilation (83), or the amount of nutrient salts available over a given period, but quantitative data are lacking. A change in the nutrient salt balance due to the mingling of river water is said (142) to be responsible for the distribution of *Laminaria ochraleuca* in the region west of the Cherbourg peninsula.

AUTECOLOGY AND RECOLONISATION

Autecology, *i.e.,* the ecological study of individual species, has in the time sequence followed upon synecology. Nearly all algal ecological studies have up to the present been synecological, and we are only now entering the phase of autecology. There is therefore an unlimited field available for future workers. Thus far work has progressed upon a few species, *e.g., Macrocystis pyrifera* (28, 265), *Saccorhiza bulbosa* (201), *Ascophyllum nodosum* (52), *Bangia fusco-purpurea* (257), *Porphyra* spp. (192) and *Chondrus crispus* (249). Even here, however, difficulties are apparent, and the study of one species in a single locality is not adequate: for example, *Ascophyllum* at Aberystwyth appears to produce one bladder and its associated thallus per season, whereas in other places (154) it may produce more.

A group of algologists in Great Britain are at present experimenting with the production of "ecological passports" for individual species; it is hoped that these may form the basis for a biological

flora which would in essence be autecological in character. An earlier attempt (157) along similar lines was too premature to be successful.

Studies on the recolonisation of artificially denuded areas (19, 52, 117, 176, 192, 261) have already shown that much valuable information can be gained, and the technique should undoubtedly be extended. It is extremely likely that such studies will throw some light upon the factors determining the characteristic zonations that can be observed. In European waters the sequence of recolonisation in the areas studied appears to be much the same, apart from one exception (117), though it may be influenced by the season of the year (192): diatoms generally return first, followed by Chlorophyceae, usually species of *Enteromorpha,* and then the Fuci, the oospores of which secure a hold in the green chlorophycean mat which is also said to provide the necessary humid environment. If the substrate is sandy the Fuci return sooner because sand provides a better foothold for the oospores than bare rock. It is interesting to note that *Ascophyllum* does not always reoccupy the same zone that it previously did but often returns at a slightly higher level (52). From studies of bared areas evidence is also forthcoming of competition between *Balanus balanoides* and *Fucus vesiculosus,* often in favour of the former.

In the Pacific the diatom stage is succeeded by a hydroid phase, then *Ectocarpus,* a pre-kelp phase, and finally the kelps return (261). In warmer waters where brown rockweeds are not present the sequence is naturally somewhat different (19). In South Africa the first two stages are the same as in Europe but the third is dominated by *Porphyra capensis.* On the warm east coast this is followed by *Ulva lactuca,* whilst on the colder west coast the next colonist is *Iridaea capensis* followed by *Splachnidium rugosum.*

How far the succession can be modified by environment has yet to be fully worked out: in at least one area (192) it is influenced by the nature of the substrate (*e.g.,* whether wood, iron or concrete), tide-level (*e.g., Ulothrix, Urospora* are the pioneers above mean sea level between March and May, and *Ulva, Porphyra* and *Enteromorpha* below), aspect, angle of slope (*Enteromorpha* occurs on vertical and *Porphyra* on horizontal iron surfaces) and competition between plants and animals (*e.g.,* algae do not appear to grow on the tubes of *Pomatoceros*). There is no doubt that further work along these lines in carefully selected areas, *e.g.,* north and south

of Cape Cod or Point Conception, or east and west of the Cape of Good Hope, would produce extremely valuable results.

GEOGRAPHICAL DISTRIBUTION

A vast field of research is still available in this direction. Publication of floras from different parts of the world proceeds, and geographical work can be founded upon them. Very little (94, 106, 108, 131, 132, 184) has been added since the pioneer work of the older algologists (22, 26, 27, 112, 113, 153, 155, 168, 226), and it is evident that here, as in nomenclature, there is the possibility of confusion arising unless future work is co-ordinated; in addition, the distribution of characteristic communities (184) has yet to be studied in detail. It is a *sine qua non* that local variations in a flora are quite insignificant as compared with the diversities that are shown by different regions. Thus the algal flora of the east and western north Atlantic and of the North Sea forms a single entity; the vegetations of the West Indies and of the Mediterranean represent two other units; the flora of the Pacific can be divided into north, central, south and so on. The warm tropical waters of the central Atlantic and Pacific form an impenetrable belt for many algae, and hence there is a marked diversity between the cold water floras of the two hemispheres.

Attempts have been made to divide the algal floras of various regions into their component elements (216, 217), but later workers (22, 27, 66, 112, 179) have not always followed the original schemes, and this is leading to confusion:

Smith (235) Setchell (216, 217) Hoyt (101)	Borgesen (22, 27) Jonsson (112)	Okamura (179)	Feldmann (66)
Boreal	Arctic		
	Sub-arctic	Subarctic	
Upper boreal	Boreal arctic	Japan & California	
	Cold boreal		
N. temperate	Warm boreal	Temperate	Boreal Atlantic
N. subtropical		Subtropical	Tropical Atlantic
		Tropical	Pan tropical
Tropical			
S. subtropical			
S. temperate			
Upper Austral			
Austral			
		Cosmopolitan	Cosmopolitan
		Indo-Pacific	Indo-Pacific
		Japan-Okhotsk	Mediterranean

It is very desirable that in the future the segregation of floras into their component elements should follow an agreed scheme. An arrangement somewhat like the following, based upon the schemes already proposed, will ultimately prove to be necessary, though doubtless additions and emendations will be forthcoming as our knowledge increases:

PROPOSED GEOGRAPHICAL ELEMENTS

Arctic	Antarctic
Subarctic	Subantarctic
Boreal arctic	Austral antarctic
Cold boreal Atlantic	Cold áustral Atlantic
Cold boreal Pacific	Cold austral Pacific
Boreal Atlantic	Boreal Pacific
Austral Atlantic	Austral Pacific
North Subtropical Atlantic	North Subtropical Pacific
South Subtropical Atlantic	South Subtropical Pacific
Tropical Atlantic	Tropical Pacific
Pantropical	Cosmopolitan
Caribbean	Arabian
Indo-Pacific	

The problem of endemism in marine algae has still to receive detailed attention. Lists of endemics have been published from various areas (20, 22, 26, 27, 65, 66, 115, 248), and these might well be studied in the light of a modified age and area hypothesis (260), bearing the limitations of the theory in mind.

Attention has been directed (245) to the existence of vicarious pairs of species and the light they can throw upon the arrangement of past land masses. One may suppose that during the glacial period in the northern hemisphere an arctic flora penetrated to France (77) and that some elements were left behind in the subsequent retreat, whilst the Baltic flora is regarded (145) as a remnant of an Atlantic flora established during the later *Littorina* period. There are many comparable problems that still require attention. Thus it is likely that the distribution of *Macrocystis* and of other algae may throw some light on the validity or otherwise of Wegener's hypothesis of continental drift. Another problem is offered in the fact that though most species of *Lessonia* are mainly circumantarctic, there is one, *L. laminarioides,* recorded from Japan and Siberia. How did this eventuate?

The important part played by temperature in controlling the

distribution of algal species has been thoroughly established (210–214, 231), and several examples are now known where there are distinct differences associated with sea-water temperature changes north and south of certain points, *e.g.,* Cape Cod (215), Point Conception (217), Coast of Spain, South Japan sea (77) and South Adriatic (204). Recently another example has been carefully and completely illustrated from South Africa (236, 237). Here the fauna and flora on the east and west coasts differ markedly, the east having a pronounced warm component and the west an equally pronounced cold water component with some species ubiquitous and a few confined to the relatively short south coast. Not only is there a difference in the composition of the vegetation, but changes in the zonation can also be followed from east to west or *vice versa.* This investigation indeed forms a model of what is wanted in other suitable parts of the world. A rather less intensive study for certain species that occur on both sides of the English Channel has produced some promising results (72). *Cystoseira ericoides* and *Bifucaria tuberculata* reach their northern limit in southern England; there they tend to be restricted to gullies and are very sensitive to changes in environmental factors. On the French coast light is regarded as the dominant factor in controlling the distribution of *Bifucaria.* In some of the species studied it is evident that a wider area would need to be considered.

Certain species of *Laminaria* and *Macrocystis* can be used as indicators of cold water currents (106, 108), whilst it is also possible, if desired, to group the algae according to their responses to temperature changes, though it is doubtful that this treatment is really successful in the light of our present knowledge. A rather specialised, though extremely interesting, subject is the distribution of the free-living forms of algae. Sometimes it is not difficult to demonstrate what happens (203), but on other occasions a peculiar form, *e.g., Pelvetia canaliculata* forma *libera,* may occur in widely separated districts (Chapman, unpub.), and this opens up many interesting problems.

Among the plankton the oceanography of the Dinoflagellate genus *Ceratium* has recently been carefully studied (86), and it has transpired that there is no correlation with salinity or temperature. There is some evidence, at present not wholly adequate, that concentration of organic metabolic products determines distribution,

whilst number of species and density are obviously related to the relative phosphate content. This type of work, however, is still in its infancy, and there is much more to be done.

LIFE-FORM

A study of life-form in the phanerogams may be a useful tool in the hand of the ecologist so long as the limitations of the method are fully realised. If a suitable life-form system for the algae could be evolved it would prove extremely useful in providing a quantitative picture of the vegetation, in comparing the floras of two or more areas, and perhaps in reflecting the type of environment. Raunkaier's system was based on the means of surviving the unfavourable season, but such a problem is not common to the majority of marine algae, though some have a narrow temperature range (213) and survive unfavourable temperatures either as spores or dwarf plants or in a denuded state. The present position has been aptly summarised (66) as follows: "Les quelques tentatives qui ont été faites à ce propos n'ont pas eu le succès désirable, et les classifications proposées jusqu' ici n'ont guère été utilisée que par ceux qui les avaient imaginées".

The earliest attempts at classification were based, as one might suppose, upon morphological criteria. The most recent developments can be regarded as dating from 1905 (182), in which bush and tree forms, net forms, whip forms, leafy forms, *etc.*, were described. Very little further progress was made until 1926 when a new wave of classifications was initiated with a scheme (216) based upon a study of coral reefs in the Pacific. This scheme also differed from the earlier one in that its basis was largely ecological: thus there were forms nestling into hollows (phloladophytes), forms growing under or in the shade of rocks (skiarophytes), surf-loving species (cumatophytes), boring algae (tranophytes) and so on. A year later another scheme was propounded (79), also based upon a study of warm-water vegetation (the Mediterranean). In this there was a reversion to the morphological basis, and it also possessed a further disadvantage in a somewhat loose terminology. Some of the groups also were based upon length of thallus, which may vary considerably for one and the same species in a single area, *e.g., Laminaria cloustoni.*

The next classification to be proposed (88) was also based upon

morphological criteria. It was, however, more ambitious because its author, realising the close inter-relationships on the shore between plants and animals, sought to make his scheme embrace both. So far as the algae were concerned the arrangement was very similar to that of 1905.

In 1931 it was suggested (123) that the criteria used for phanerogams, *e.g.*, method of perennation, could be employed. The scheme was not extended into any detail, and the four primary groups (perennials, pseudo-perennials, annuals, casual annuals) would require considerable subdivision. If method of perennation is to be adopted as the most favourable arrangement, then the classification suggested in 1937 (66) must be regarded as the most satisfactory so far produced. This is perhaps worth reproducing:

ANNUALS

a. Species found throughout the year: spores or oospores germinate immediately. Ephemerophyceae, *e.g., Cladophora* sp.
b. Species found during part of the year only.
  i. Algae present during the rest of the year as a microscopic thallus. Eclipsiophyceae, *e.g., Ectocarpus, Litosiphon.*
  ii. Algae passing the unfavourable season in a resting stage. Hypnophyceae, *e.g., Nostoc, Coleochaete, Ulothrix, Porphyra, Dudresnaya.*

PERENNIALS

a. Found entire throughout the year
  i. Frond erect. Phanerophyceae, *e.g., Fucus, Sargassum.*
  ii. Frond a crust. Chamaephyceae, *e.g., Peyssonnelia.*
b. Only a portion of the frond persisting a whole year
  i. Part of the erect frond disappears. Hemiphanerophyceae, *e.g., Himathalia.*
  ii. Basal portion of thallus persists. Hemicryptophyceae, *e.g., Cladostephus, Corallina.*

The success of such a classification would depend on the importance that may be ascribed to perennation in an environment where conditions are generally extremely uniform. The ideas and terminology that have proved successful for the angiosperms may not be equally satisfactory for such a wholly different group as the algae. The present reviewer is inclined to the opinion that a classification based upon environment or mode of life is likely to prove more successful and more useful to ecologists. Furthermore, any system of life-form for algae should include the fresh-water and terrestrial species, if it is to be complete, and the majority of schemes so far proposed are lacking in this respect. A scheme propounded in 1939 (33) is admirable in so far as it applies to fresh water and

terrestrial forms, and if these ideas could be incorporated in a general scheme the result should approach what is really required.

It is probable, therefore, that a scheme somewhat on the lines of that propounded by Setchell (216) and combined with that of Cedergren (33) would form a useful synthesis. At present there is no doubt that a satisfactory life-form scheme has yet to be devised. No serious attempt has been made to construct biological spectra for different regions, although the reviewer has attempted this (unpublished), using a life-form scheme that is a modification of Feldmann's. Certain features emerge from comparisons of different areas. Thus rocky sea shores are characterised by a high percentage of annuals and epiphytes, salt marshes by a high percentage of free-living forms and soil algae, bodies of fresh water by a high proportion of plankton (small forms) and pleuston (large floating forms), and warm marine regions by numerous calcareous forms. Apart from its value in comparing the floras of different regions there is good reason to believe that a successful scheme would also be very useful in comparing the vegetation belts at different levels on the sea shore.

NOMENCLATURE

The present usage of nomenclature in marine algal ecology is rapidly leading towards chaos, and it is most important that some authoritative decisions be reached in the near future, as an earlier attempt (111) was too premature. At present investigators adopt their own nomenclature which is generally some variant of the terminology used in land ecology. There are two main problems here which need to be solved. There is first the delimitation of the regions of the shore, *e.g.*, littoral, supralittoral and infra- or sublittoral (119), and then there is the nomenclature to be applied to the communities and belts of vegetation. In the latter case we are required to decide whether the terms used in land ecological practice should be retained, or whether the conditions are such, *i.e.*, the close inter-dependence of plants and animals (255), that a completely new set of terms should be introduced. If the former procedure is adopted it is important that workers in this field agree about the nature of the vegetation with which they are dealing, *e.g.*, does the vegetation represent a climax or is it fundamentally seral in character? The individualistic concept (89) has not been

generally adopted by ecologists, and there seems no reason to believe that it would specially apply on the seashore.

Delimitation of the regions of the shore has been brought into confusion by the frequent use of the vegetation for purposes of demarcation (208). This is unsatisfactory (88), even if the vegetation is correlated with the physical conditions. Here it is more important than ever that there should be agreement between botanist and zoologist. In the past the boundary between the *Fucus serratus* and the *Laminaria* or red algal zone has often been regarded as marking the lower limit of the littoral. Some zoologists, on the other hand, have placed this lower limit at 40 metres (3) or even deeper (29). The portion of the shore, the littoral, that is exposed daily is obviously an important region, and yet its boundaries are almost as hard to fix as those of a species. If it is based upon physical characters the upper limit is often regarded as being normal high water line (208), but this would seem to be far too ambiguous. It could, for example, refer to high water mark of ordinary tides (*e.g.,* mean average tides), or it could apply to high water mark of ordinary spring tides. Another modification (128) is associated with the raising of the upper boundary through wave action (spray), thus giving what is termed a physiological high water mark or "litus" line (228). The spray zone (45, 109) could equally well be placed in the littoral or in the supra-littoral (66, 187). It probably matters little which usage is adopted so long as we can achieve some degree of uniformity and reduce the personal element. At present it would seem that a littoral extending from H.W.M. to L.W.M. of average spring tides would satisfy most workers. There would seem to be no reason for introducing such terms as "wash zone" (always covered), "splash zone" (areas where waves break) and "spray zone" (45), even though these do emphasise the effect of the tides. The use of L.W.M. of neap tides (88) for the lower limit would seem to be incongruous, though this is adopted by some workers. Even the definitions given above are not wholly satisfactory, and ultimately the best method for defining the littoral, when data are available, will be as that area lying between an upper limit with more than x submergences per annum and a lower limit with more than y emergences. A careful study is required in order to determine the exact values of x and y. In areas, such as the Baltic, where there is no

tide, the term "littoral" is commonly applied to the zone that is uncovered during the summer fall of water level or to 0.5 metre below M.L.W. (227). This usage will only lead to confusion, and a special term, such as "seasonal exposure zone", is obviously required.

Whatever definition of the littoral be finally adopted it is likely that there will be a zone between the lower limit and extreme L.W.M. of spring tides where there will be occasional exposure. It will probably prove desirable to regard this as an independent zone, the lower littoral or the upper sub-littoral. At the other end of the vertical scale the supra-littoral will extend upwards from H.W.M. of average spring tides and will include the spray zone and the region covered by storm and equinoctial tides. The upper limit of the supra-littoral will therefore vary from place to place, depending on exposure and protection, and will be determined by extreme H.W.M. of spring tides or the upper limit of the spray zone. The lower limit of the halophilous phanerogams has been suggested (66) as the demarcation line, but this would not operate in a salt marsh or mangrove area.

Below the littoral is the sublittoral. In certain areas this has been subdivided (4, 66, 147, 187), but a gradation is usually discernible, and this practice ought to be abandoned. Some workers have placed the lower limit of this zone at the depth where the algal covering ceases to be continuous, whilst others (21, 199) have adopted the lowest depth to which attached algae can penetrate. Another suggestion for the lower limit has been the line where sedentary animals commence to dominate the algae (88). In the tropics animals tend to be more abundant than algae from the lower littoral downwards, and so the lower boundary of coral reefs has been suggested as a useful means of marking the sublittoral (88). The confusion that can be caused by adoption of botanical or zoological subdivisions is immense (228), and it is evident that the lower limit of the sublittoral requires to be placed on a purely physical basis, *e.g.*, the percentage of light penetration. The limits cannot therefore be regarded as fixed conclusively, and further work on physical constants in relation to flora and fauna is necessary.

The sublittoral is succeeded by the elittoral which is regarded as extending down to the lower limit of plant life (66, 208), but this definition is complicated because some authors make a distinction

between microscopic and macroscopic plant life (88). In the tropics this criterion has not been used, and in its place the lower limit of *Lithothamnia,* between 38 and 100 fathoms, has been proposed in its place. This is obviously related (69, 76) to a photic factor, and again it is desirable that this limit be based on a purely physical rather than on a biological basis.

Below the elittoral a continental or archibenthal region has been recognised, although it has been suggested that there is an intermediate profundal or sub-elittoral region characterised by the presence of dead vegetable nutriment. Finally the lowest region is the abyssal. The vertical extent of all these regions will vary from place to place, and at present data are greatly required.

Turning now to the other problem of nomenclature, a full appreciation of the position can be achieved only after a brief survey of past developments. The first attempt at marine sociology can be said to date back to 1812 (256), but in 1832 an important contribution (5) was made in which the close interdependence of plants and animals was recognised. This work had a considerable influence upon contemporary thought and was followed by many workers, especially on the continent of Europe, for over half a century. Somewhat later a monumental work (147) on the Adriatic fauna and flora appeared, dealing with both in considerable detail, whilst similar studies (75) appeared for Great Britain and France (250). Ten years later the first use of the term "biocenose" appeared in the literature when it was coined to describe the biotic community which is such a feature of the sea-shore. From 1860 to 1890 numerous works appeared by Scandinavian authors (90, 95, 126, 193, 199, 224, 225) who described many algal formations and associations. Most of these were modelled on an early work (119), and this unfortunately introduced the confusion in terminology that has never since been wholly rectified. The formation was defined (119) as "a small portion of the whole algal vegetation and characterised by the type of vegetation; generally they obtain their characteristic stamp through one or more of the predominant algae". This represents a grave departure from current ecological practice, and what the Scandinavians often termed a "formation" would today be regarded as an "association" or "consociation". This was, in fact, emphasised by a later writer (259) who, at the same time, propounded a scheme that was far too generalised. Some of the

later Scandinavian workers (20, 21, 112, 128, 207) modified these earlier ideas, and one finds descriptions of Fucaceae and Chlorophyceae formations each containing one or more associations. It is important to notice, however, that with but few exceptions all the associations were characterised by the presence of a single dominant. The term "association" cannot correctly (140) be employed for a complex group such as the Fucaceae association (45) because the environmental conditions between the upper and lower species vary so widely. Whether the *Laminaria* association should likewise be discarded is very much more questionable because the species intermingle much more. Another anomalous treatment was used in describing the associations of San Juan (166) where a single name was given to a community containing more than one dominant. Formations were also sometimes regarded as composed of associations united together under the same or nearly the same ecological conditions; such aggregations are better described as belts.

After 1900 the majority of algal ecological workers adopted the terminology used by the Scandinavians, or else they employed (1, 84, 85) the non-committal term of "community". This term is preferable to the incorrect usage of other ecological terms. Introduction of more terms was probably inevitable, and so we find "modes" based upon degrees of salinity and degrees of exposure and "facies" based upon variations of substrate (8–10). Later the word "facies" (9) became used for portions of associations dominated by secondary species or modified by exposure (158, 181, 187). It was then (88) pointed out that the word "facies" was originally introduced by geologists to indicate differences in ground and therefore should not be used in any other sense. In recent works (65, 66) it has been employed in its proper geological sense, and it has been replaced by the term "fasciation" (223) to describe modifications of the association.

Terms have also been employed incorrectly. Thus "zone" has been employed for "association" and "association" for "fasciation". Additional confusion in terminology has often resulted from a too detailed analysis of a small region, with the result that far too many communities have been described with the status of an association. In one case no less than 57 algal associations were described from Woods Hole (53).

The concept of the biotic community has received rather more

attention since 1900. Quite early biocenoses were discussed by zoologists in relation to differences of environment, and some biocenoses were also described from northern Germany (175) and Sweden (197, 198). Before considering this phase of development in more detail mention must be made of a very important paper (49) which has exerted a profound influence upon algal ecology. The most significant departure from previous practice was the basing of formations upon differences of substrate, *e.g.,* rock, sand, mud, salt marsh, whilst exposure and protection were also involved. A number of subsequent authors followed this example of nomenclature (91, 116, 117), but it is important to remember that at least two leading ecologists (112, 246) have specifically stated that the term "formation" should not be used in any other sense than that in which it is used for land vegetation, and that, however tempting it may be to name the association after the habitat, nevertheless the name should be based upon the dominant plant or animal species.

About 1924 two very important contributions (88, 180) appeared in which the biocenose concept played a prominent part. In New Zealand eight formations were described, each composed of a number of subformations or associations, though many of the latter were characterised by only one dominant. There was a tendency also to restrict the animals and plants to separate formations, whereas animals and plants can be co-dominant and co-extensive, *e.g.,* a *Novastoa*-encrusting coralline association (50). In the second paper on Gullmar Fiord an association was defined as "a combination of species where one or more forms predominate so that the community gets a biotically determined "physiognomy". Usually, however, the associations there described possessed only one dominant. The term "variation" was introduced to describe modifications within an association, but in view of its accepted usage in genetics this term must be discarded in favour of "fasciation" or some other term. An horizontally extended association was called a "belt" and a vertical group of associations were collectively known as an "association complex". It was pointed out that the biocenoses were often two-layered, so that one had the equivalent of synusiae. Epiphytes formed a distinct problem, and though it was admitted that they might characterise an association, nevertheless they were commonly classed as variations (= fasciations).

These ideas all formed an important contribution to marine ecology, and they have been employed in at least one subsequent paper (50).

Since then a number of workers (39, 45, 109, 238) have insisted that the extensive belts on the shore are primarily based upon tidal phenomena, and one should not therefore use plant names for them, as the species may vary from place to place. At present our information is not sufficient to enable us to say exactly how the belts could best be delineated and named. The reviewer believes that ultimately they will have to be based upon either degree of exposure or upon critical levels (45, 52). One definition of the term "association" (192) is indicative of these ideas, though at present it is scarcely practicable. The association is defined as composed of dominants accompanied by other species whose presence is determined by responses to factors similar to those influencing the dominants. There is no doubt that this is one aspect of the subject in which considerable advances may be expected.

From 1930 onwards ecological accounts describing associations, usually with one dominant, from a number of areas have appeared (34, 52, 56, 66, 84, 85, 91, 140, 145, 192, 198, 218–220, 264). The influence of earlier work (49) is still evident (34, 145, 192) in a number of the contributions, but in some of them new ideas have been introduced. Thus it has been realised that if the vegetation of a rocky shore is regarded as a climax vegetation then one should employ the ecological terms "consociation", "society", *etc.* (34, 52, 195–198), though even these have not always been used correctly. The word "society" has been employed not only for local dominance of a subsidiary species but also to mark seasonal dominance (192). It is desirable that these two phenomena be regarded as distinct and the term "aspect" be applied to cases of seasonal dominance.

Some workers apparently do not recognise the existence of formations (1, 65, 66, 84, 85), whilst, by way of contrast, a very recent paper (232) describes in considerable detail the formations to be found in South America and the Subantarctic. These formations, which are based upon life-form or locality, are as follows:

1. Upper littoral formation of drought-resistant algae.
2. Lower littoral formation of surf-resistant Rhodophyceae.
3. Lower littoral formation on sheltered coasts.
4. Surf formation of larger Phaeophyceae.
5. Formation of large submarine Phaeophyceae.

6. Formation of giant Phaeophyceae with buoy-carried fronds.
7. Formation of deep-water Rhodophyceae.
8. Formation of crustaceous corallines.

If normal ecological practice were followed it is clear that many of the above are too small to warrant formation status.

The two most important recent contributions are both the work of zoologists (223, 236, 237) who, in general, consider that animals are of prime significance and that the algae merely mark fasciations of the animal communities. This view is probably too extreme, though it is being adopted by others (2). One group of workers (223) recognised four principal biomes, each containing a number of associations, whilst fasciation was employed for modifications of associations resulting from loss of or addition to the important species. Stephenson (236, 237) has a much wider approach to the whole subject because he rightly demands that a system be evolved that is, so far as possible, applicable to the whole inter-tidal region of the world, and he has made a first attempt with the inter-tidal regions of South Africa and Scotland. The same worker also advocates use of tides as a means of delimiting the zones, but he points out that until more tidal data are available we shall perforce have to employ biological units.

There is much less comparable work on the algal ecology of salt marshes, either because it is not so attractive or because it is more difficult. Earlier workers (49, 110) adopted the terminology used for rocky shores, whilst later workers (192) have either followed this usage or used the non-committal term of community (32). It was not until recently (36, 37) that the dynamic nature of the algal vegetation on salt marshes was emphasized and seral terminology introduced.

From the above all-too-brief summary it is clear that in the past there have been three views, from

a) those who base their terminology upon habitat
b) those who stress large units (mainly zoologists)
c) those who stress small units (mainly algologists)

There is, therefore, the problem of whether terminology should be based upon habitat or whether existing ecological terminology, as applied to land vegetation, should be employed more strictly than it obviously has been in the past. If the former view is adopted then a new terminology would need to be evolved[5] in order to avoid con-

[5] New concepts for existing terms (140) would be unsatisfactory.

fusion, but there seems little or no reason why existing ecological practice should not be maintained. If this second viewpoint is accepted then any difficulty of having to decide between the alternatives *b* and *c* above will automatically disappear. The reviewer strongly recommends maintenance of normal ecological practice using the definitions given in a standard text (247). Associations will then be characterised by more than one dominant, consociations by one dominant, societies by a locally dominant secondary species, and so on. The term "aspect" should be used for seasonal communities, and the term "fasciation" need no longer be employed. The word "zone" should be left to the phytogeographers and "belt" employed for the horizontal bands along the shore; "storey" could also then be abandoned. Ultimately our aim should be to characterise the belts by physical features, *e.g.*, degree of exposure, expressed either as a percentage or in terms of maximum periods of non-tidal exposure (39).

The vegetation of the rocky shore is probably best regarded as representing climax vegetation, although it could be regarded as a number of secondary successions because the life of the components of the vegetation is short-lived. This, however, is purely relative, for an oakwood could be regarded in the same light, though the length of time before complete regeneration occurs is longer. Climax terminology should therefore be used on rocky shores, and the following outline is suggested as a possible scheme upon which marine ecologists, both botanical and zoological, might base discussions (purely animal formations are neglected):

A. Large brown rockweed formation type.
   1. North Atlantic large brown rockweed formation.
      a) Exposed coast complex
      b) Sheltered coast complex
         Balanus—Pelvetia canaliculata association
         Littorina—Fucus spiralis association
         Ascophyllum—F. vesiculosus association
         Balanus—F. serratus—Chondrus association

   The associations will each contain one or more consociations and societies together with some seasonal aspects.

   2. North Pacific large brown rockweed formation.
   3. South Pacific large brown rockweed formation.

   (Both these would be subdivided as in 1.)

B. Large submerged Phaeophyceae Formation type.
   1. North Atlantic *Laminaria* formation.
   2. North Pacific kelp formation.
   3. South Pacific kelp formation.
   4. South Atlantic kelp formation.
   5. *Sargassum* formation.

C. Coral Formation type.
   1. West Indies Coral formation.
   2. Indo-Malayan Coral formation.
   3. Central Pacific Coral formation.
   4. Australian Coral formation.

Both B and C would be subdivided into associations dominated by plants or animals or by both.

We know very little about the status of the algal communities on sandy shores and in estuaries, and until more work is available one cannot say whether they should be regarded as climax or seral vegetation. The algal vegetation of salt marshes and mangrove swamps is clearly seral in character, and nomenclatural practice should follow the usual rules. Thus for salt marsh algal vegetation one can postulate the existence of a North Atlantic sere, Baltic sere, Northwest Pacific sere, South Pacific sere, Western Mangrove sere, Indo-Malayan mangrove sere and perhaps others. These seres will be composed of a number of associes, consocies and socies, and in describing these it may be necessary to consider the algae together with the phanerogams; but as animals are commonly not predominant they will rarely enter into the naming of the large units.

CONCLUSIONS

One can regard marine algal ecology as being at a parting of the ways. Much will depend on the type and nature of the work in the immediate future. Some degree of co-ordination is a necessity, and in this subject more than anywhere else there is need of teamwork between animal and plant ecologists and the systematist. The close inter-relations between plants and animals on the sea shore demand that future work be teamwork; only thus will a final and satisfactory solution of nomenclatural problems be achieved. Ecologists have been criticised (183) for this lack of co-ordination, and marine ecologists are perhaps most guilty. Synecological studies will finally be understood only if they are succeeded by adequate autecological studies, and the time is now ripe for a definite attack on the individual species. Generally speaking, synecology has, up to the present, been concerned with relatively small areas, and future workers should aim at co-ordinating their results with those of their predecessors and co-workers. It is evident that many gaps in our knowledge remain, some of them fundamental in character, and these must be filled. In particular we require much

more information about the tidal phenomena on all types of coast; we need information about the types of algal communities that exist in muddy bays, sandy shores and mangrove swamps. Insufficient attention in the past has also been paid to the smaller algae, especially members of the Cryptophyceae, Chrysophyceae and Myxophyceae, and there is no doubt that much remains to be discovered of the part played by these algae in the tropics, although some data are already available (18, 60).

Further study of physiological races in relation to distribution and environmental factors will be of considerable importance, whilst the development of a workable life-form scheme may indicate additional avenues for profitable research.

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